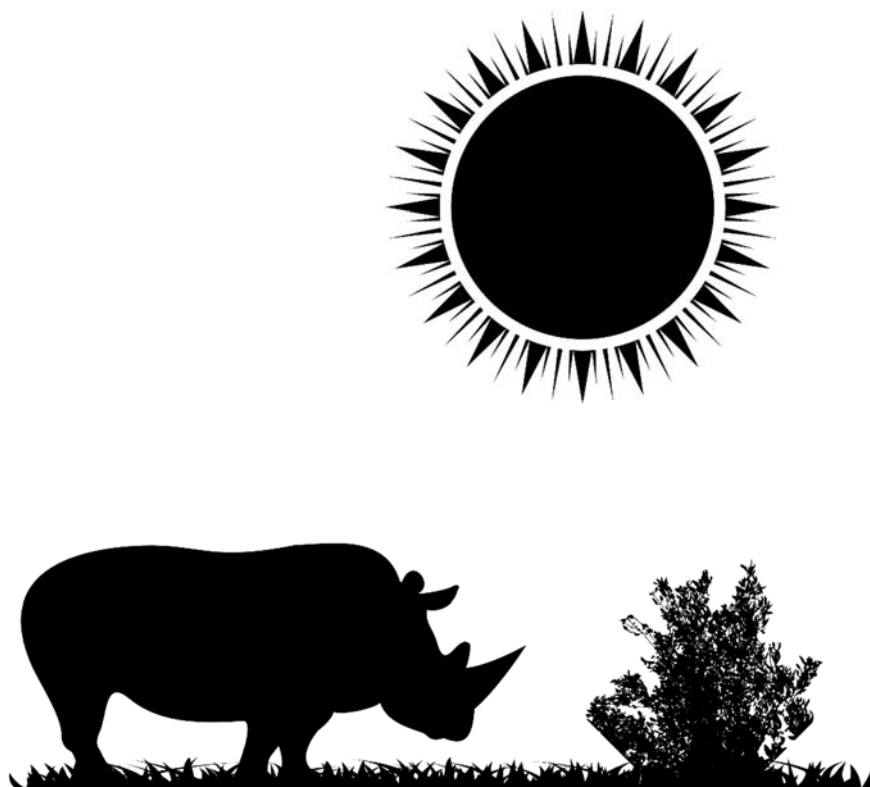


# **Grazing impacts on savanna vegetation states and its role in albedo changes**

**Joana Fernandes**



**Master's thesis • 60 credits**

Management of Fish and Wildlife Populations

Examensarbete/Master's thesis, 2018:4

Department of Wildlife, Fish, and Environmental Studies

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# Grazing impacts on savanna vegetation states and its role in albedo changes

Joana Fernandes

**Supervisor:** Joris Cromsigt, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies  
**Assistant supervisor:** Mariska te Beest, Wageningen University, Resource Ecology Group  
**Examiner:** Joakim Hjältén, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

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**Swedish University of Agricultural Sciences**  
Faculty of Forest Sciences  
Department of Wildlife, Fish, and Environmental Studies



## Abstract

Albedo, i.e., the fraction of the incoming sunlight that a surface reflects, has been previously shown to play a key role on the climate system by influencing the energy balance of the Earth's ecosystems. Shifts in land cover, such as deforestation for agriculture, or the creation of grazing lawns by grazers, are likely to alter albedo, which, in turn, can influence the local climate - higher albedos are associated with a net cooling effect, while lower albedos can lead to surface temperature increases. Raises in temperature have been previously linked to woody encroachment, process that can further lead to a warmer effect due to the reduced albedo of woody plants in comparison with grass. In the present study, I investigated how albedo differed between three distinct savanna vegetation types: grazing lawns, tall bunch grassland and woody encroached tall grassland. I showed that grazing lawns have a significantly higher albedo than woody encroached tall grass. Albedo decreased with the amount of bare soil, and increased with the amount of grass. However, it was not affected by woody cover. I also investigated the likelihood of shrub encroachment to happen in lawns and tall bunch grass, and found that it happens more easily in tall bunch grass. This study supports that grazers, particularly megaherbivores, as main drivers of grazing lawns formation and maintenance, can affect the local climate of African savannas. By creating grazing lawns, herbivores also prevent shrub encroachment and the changes in albedo (and consequently, in local climate) that this process provokes. Another important aspect of this study is to supply more empirical data on the importance of a megaherbivore, such as white rhino, to the ecosystem and the possible consequences of its removal, which in light of the recent poaching crisis might be a reality not so far away.

# 1 Introduction

Changes in ecosystems, such as alterations in land cover, can strongly impact the climate system (Foley et al., 2003, Hoffmann and Jackson, 2000, Syktus and McAlpine, 2016). Vegetation interacts with climate through a variety of mechanisms - biochemical feedbacks (carbon cycle) and biophysical feedbacks (water and energy cycles) (Chapin et al., 2008). Carbon dioxide released by human activities has been regarded as a major contributor to the greenhouse effect and consequently as the main responsible driver of climate change. Forests are known for their capacity to sequester carbon from the atmosphere, which can potentially counteract fossil fuel emissions (Alkama and Cescatti, 2016), and forest management is a frequently proposed strategy to decelerate global warming (Naudts et al., 2016). However, the biophysical feedbacks should also be taken into consideration when developing climate change mitigation protocols (Syktus and McAlpine, 2016, Foley et al., 2003, Bonan, 2008). In fact, using climate models, Bala et al. (2007) demonstrated that global-scale deforestation had a net cooling, not warming, effect on climate – although the loss of carbon dioxide due to the loss of trees exerted a warming effect, this effect was counteracted by the net cooling effect provoked by changes in evapotranspiration and albedo (Betts, 2000, Bonan, 2008).

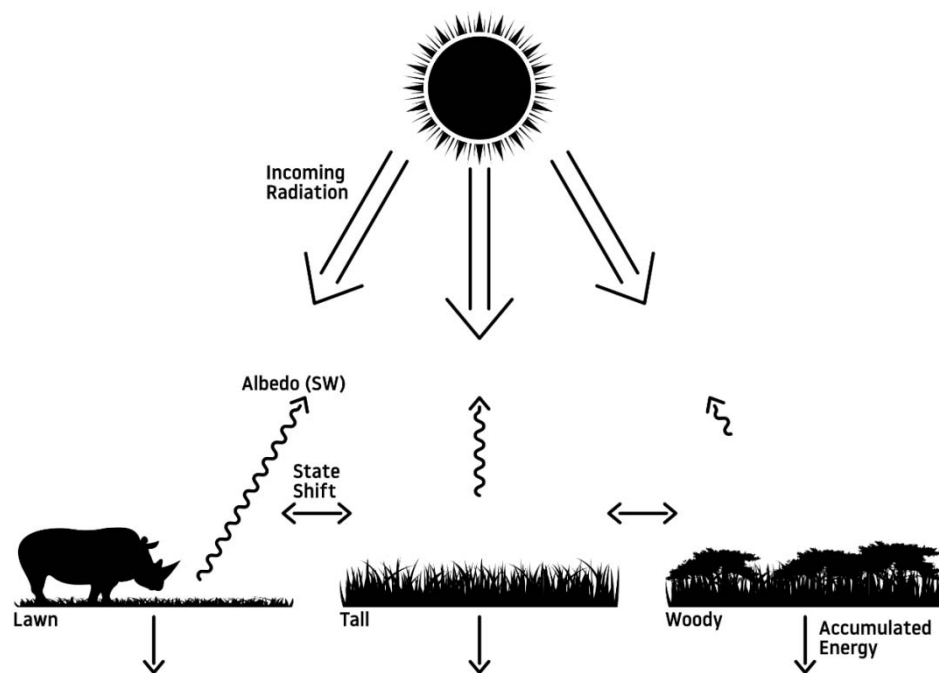
An increasing number of studies shows that not only carbon dynamics are important for climate change. Albedo, i.e., the fraction of the incoming sunlight that a surface reflects (A Coakley, 2003), also plays a key role by influencing the energy balance of the Earth's ecosystems (Cohen et al., 2013, Foley et al., 2003, Betts, 2000, Alkama and Cescatti, 2016). The relevance of the biochemical and biophysical effects seems to be different according to latitude, with the effect of albedo being larger at higher latitudes, while the transpiration and carbon feedbacks are more important in the tropics (Bala et al., 2007, Chapin et al., 2008). Albedo is not an intrinsic and static property of a surface since it depends on the atmospheric composition (e.g. presence of clouds), the direction and the touching surface of the incoming light (A Coakley, 2003). Hence it varies between surfaces, with oceans and forests having a relatively lower albedo than deserts and grasslands (Bala et al., 2007, Allen et al., 1994, Beringer et al., 2005), which means more energy is absorbed by wooded systems than by grasslands. Because the fraction of light which is not reflected is then absorbed by the surface, it leads, among other processes, to surface temperature increases (A Coakley, 2003). The lower albedo in forests can be attributed to the more complex canopies of trees and shrubs that are able to trap a higher percentage of shortwave radiation (Chapin et al., 2000,

Beringer et al., 2005). An implication of this would be that (short) grass patches without woody components should reflect more radiation and therefore reduce warming. Raises in temperature have previously been linked to woody expansion (Auken, 2000, Tape et al., 2006, Sturm et al., 2001), which according to Stevens et al. (2017) has been increasing since the 1970s in savannas across the world.

Herbivores can contribute to variation in albedo by modifying land cover. As shown by Cohen et al (2013) and te Beest et al. (2016), grazing pressure by reindeer in the tundra led to a decrease in shrub density, which consequently delayed snowmelt and increased surface albedo. Similarly, Doughty *et al.* (2010) suggested that the collapse of mammoth populations during the Pleistocene led to the expansion of dwarf shrubs, which led to decreased albedo and increased warming. Megaherbivores may play a similar role in extant ecosystems. Megaherbivores are those herbivores whose body mass exceeds 1000 kgs as adults, including elephants, hippopotamus and white rhinoceros (Owen-Smith, 1988). According to Paine (1995), megaherbivores are keystone species, because they have a disproportionate impact on their habitats. Previous studies recognized their importance in shaping the structure of savanna ecosystems (Cromsigt and te Beest, 2014), by influencing the abundance of different vegetation states.

One important feature of savanna landscapes is the existence of grazing lawns, defined by McNaughton (1984) as ‘areas created and maintained by grazers’. These areas support a high diversity of grazers (Archibald et al., 2005), because they offer high resource availability, with a higher number of palatable grass species, and this high forage quality is what promotes recurrent grazing (Cromsigt and Kuiper 2011). At the same time, regular grazing is an essential component of grazing lawns dynamics since it prevents the colonization by tall bunch grass species (Hempson et al., 2015). In Kruger National Park, Cromsigt and te Beest (2014) found that grazing lawns were mostly absent in areas with low white rhino densities, and the proportion of short grass was 60 to 80 % lower than in areas with high white rhino densities. Similarly, Waldram et al. (2008) identified white rhinos as an important driver of grazing lawns abundance in Hluhluwe-iMfolozi Park, showing that, in the absence of rhinos, other grazers species were unable to maintain patches of lawn in mesic Hluhluwe. Furthermore, by maintaining these patches of grazing lawns, white rhino may prevent shrub encroachment of savanna grassland (Stevens et al., 2017). It has been suggested that woody recruitment was more constrained in grazing lawns, because herbivores are better able to find and eat up the seedlings in lawns. Also, the soil is drier in grazing lawns than in tall bunch grassland, which can also difficult woody plants recruitment (van der Waal et al., 2011). Since shrub encroachment, as mentioned before, could lead to

decreases in albedo and subsequently to surface temperature increases (te Beest et al., 2016), white rhino might play an important role in cooling the local climate. The purpose of this study is to investigate how different white rhino-mediated vegetation states in Hluhluwe-iMfolozi Park, South Africa, differ in albedo (Figure 1). By creating grazing lawns, rhinos might also be preventing shrub encroachment. Therefore, I predict shrub encroachment happens more easily in tall bunch grass. I hypothesized that grazing lawns will have a higher albedo than tall bunch grass and woody encroached tall grassland. I also hypothesized that the presence of woody plants encroached in tall bunch grassland will be higher than in grazing lawns.



*Figure 1.* Schematic representation of vegetation shifts and energy feedbacks: white rhino-mediated vegetation states influence albedo, with grazing lawns reflecting more radiation than tall bunch grassland and woody encroached tall grassland.



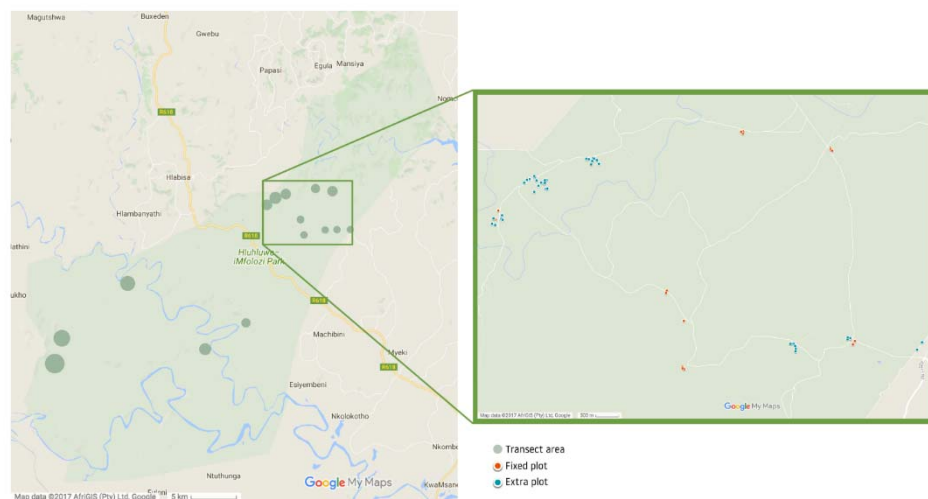
## 2 Materials & Methods

### 2.1 Study area

The study was conducted in Hluhluwe iMfolozi Park (HiP), KwaZulu-Natal, South Africa (Figure 2). This fenced park, located on the east coast of South Africa between 28°00'S and 28°26'S; 31°43'E and 32°09'E, today includes a total area of around 90,000 ha. Initially, this area was split in Hluhluwe Game Reserve and Umfolozi Game Reserve, which were among the first protected areas in Africa, and a corridor connecting both reserves. Several changes occurred throughout the years, and the two reserves were eventually united with the incorporation of the corridor, forming in 1985 the Hluhluwe-iMfolozi Park that we know today (Brooks and Macdonald, 1983). This region has a coastally modified climate with a wet summer (October to March) and dry winter (April to September) (Boundja and Midgley, 2010, Cromsigt, 2006). The mean annual rainfall varies between 635 mm and 990 mm depending on altitude, which spans a gradient of 60-750 m (Balfour and Howison, 2002). The northern, Hluhluwe, and the southern, iMfolozi, parts vary significantly in climate and topography (Boundja and Midgley, 2010). Hluhluwe is mostly covered by mesic savanna with steep hills and mean annual rainfall of 985 mm, while iMfolozi is dominated by semi-arid savanna with less pronounced elevational gradients, with broad flood plains, and a mean annual rainfall of 650 mm (Cromsigt and Olff, 2006, Waldram et al., 2008, Linklater and Hutcheson, 2010). The temperature within HiP ranges from 13°C to 35°C.

The park predominantly consists of mudstone soils, but granite-, arenite- and basalt-derived soils can also be found in high altitude areas (Whateley and Porter, 1983, Cromsigt, 2006). Vegetation in the park is very heterogeneous, ranging from open grasslands to closed Acacia woodlands and thickets of dense broadleaf species (Owen-Smith, 2004, Whateley and Porter, 1983). Grasslands are a mix of tall bunch grasses (mainly *Themeda triandra*, *Sporobolus pyramidalis*, *Eragrostis curvula*, and *Panicum maximum* communities) and short stoloniferous grazing lawns (mainly *Digitaria longiflora*, *Urochloa mosambicensis*, *Dactyloctenium australe* and *Sporobolus nitens* (Cromsigt and Olff, 2008, Waldram et al., 2008). The park is home to a very diverse mammal community, including herbivores and carnivores. The herbivore community has fluctuated markedly over the years, due to disease outbreaks and management interventions, such as culling operations. There have been two massive culling operations, one during the 1930s and 1940s

for disease control as part of an anti-Tsetse fly campaign, and a second during the 1960s to 1980s to reduce perceived overgrazing during a period of severe drought (Brooks and Macdonald, 1983). White rhinos were protected during these campaigns, and with the start of the so-called ‘Operation rhino’ in 1969, rhinos were removed from the park through live removal and reintroduced in other protected areas. Since the park was one of the last places hosting individuals of this species, this operation arose to prevent white rhino extinction (Le Roux et al., 2017). Hluhluwe-iMfolozi Park has since played a key role in rhino conservation, allowing, for example, the reintroduction of rhinos to the Kruger National Park (Pienaar 1970). According to Gaisford and Swart (2010), ‘every single Southern white rhino population in the world has its genetic origin in the Hluhluwe-iMfolozi Park’. In HiP, white-rhinos play a central role in grazing, consuming over one third of the grass eaten by all large herbivores (Cromsigt et al., 2017). Since the 1980s herbivore management practices have changed and allowed herbivore populations to grow, so that nowadays a vast diversity of native herbivores reaches a total herbivore biomass exceeding 10 000 kg/km<sup>2</sup> (Le Roux et al., 2017), which is twice the biomass in Kruger National Park. Common species are impala (*Aepyceros melampus*), common warthog (*Phacochoerus africanus*), blue wildebeest (*Connochaetes taurinus*), common zebra (*Equus burchellii*), African buffalo (*Syncerus caffer*), African elephant (*Loxodonta Africana*), giraffe (*Giraffa camelopardalis*) and white rhino (*Ceratotherium simum simum*) (Cromsigt 2006).



**Figure 2.** Outline of the Hluhluwe-iMfolozi Park map showing the position of the albedo measurement plots and the transects’ areas. Every site includes three plots. Due to the zoom, some plots are clustered together, so they show as one or two points on the map. The seventy-nine transects were not represented individually but rather as areas for better clarity. The size of the circles represents the density of transects in each area.

## 2.2 Data Sampling

### 2.2.1 Study I: linking albedo to vegetation states

#### *Study design*

I selected a total of 20 sites distributed over the northern part of the park (Figure 2). Six of these sites had been previously established in another study (Vedin, 2016) and will from now on be referred to as ‘fixed sites’. The purpose of the fixed sites was to measure variation in albedo over time and to see whether differences among vegetation types in albedo varied over time. The remaining 14 sites, from here on called ‘extra sites’, were chosen particularly for the present study to look at albedo variation among plots with a clear contrast in vegetation types for a larger number of sites. The extra sites were chosen following the same criteria as for the fixed sites and the only difference between fixed and extra sites was the frequency of measurement — the latter were only visited once, while the former were visited every month between October 2016 and May 2017. Otherwise, the measurements and protocols were the same for both. In each site, there were 3 plots, at least 100 meters apart from one another, representing three different grassland types: grazing lawn, tall bunch grassland and woody encroached tall grassland (Figure 3). A grazing lawn plot was characterized by the dominant presence of short prostrate-growing lawn-type grass species, such as *Digitaria longiflora*, *Sporobolus nitens* and *Urochloa mosambicensis*. Tall grassland plots were defined by grass growing in tall grass tufts, including dominant species such as *Panicum maximum*, *Themeda triandra* and *Sporobolus pyramidalis*. The third type of plot was defined as tall grassland plots that were encroached by woody plants such as *Dichrostachys cinerea* and *Maytenus senegalensis*. Due to the fact that the albedometer range of measurement is circular, plots were defined as circles of 2.6 meters radius.



*Figure 3.* The three vegetation types assessed during this study. From left to right: grazing lawn, tall grassland and woody encroached tall grassland.

### *Albedo measurements*

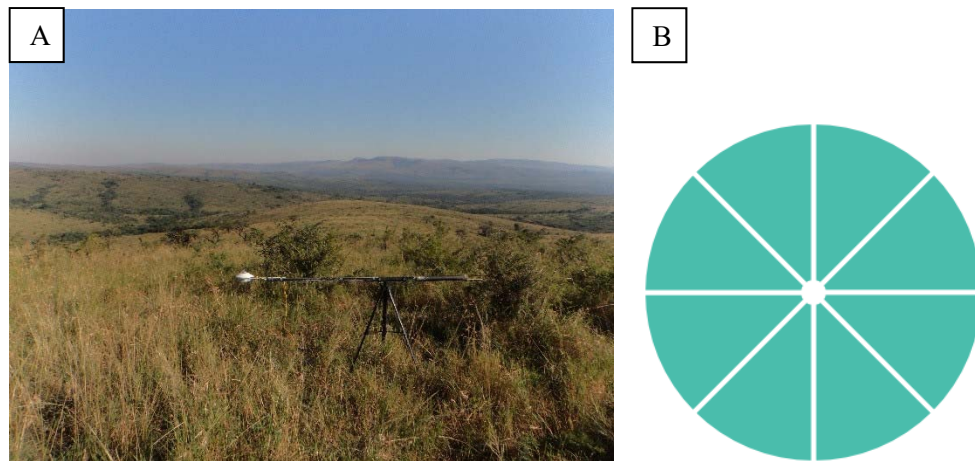
I used an albedometer (upward and downward facing CMP11 pyranometers, CMA11, Kipp & Zonen, Delft, the Netherlands) that was sensitive to short wave radiation between 285 and 2800 nm and positioned it one meter above the ground using a tripod at the center of each plot following Williamson *et al.* (2016) (Figure 4A). Measurements were taken between 9 am and 3 pm, since there is minor variation in albedo values during this period (see Vedin, 2016). Moreover, within each site all plots were measured within one hour of each other to avoid any potential influence of the solar angle on albedo. I started to record albedo for 10 minutes, as Vedin (2016) did in her study, but since there was no variation in albedo over that period neither in Vedin's data or mine, I shortened the measurement time to 5 minutes. The logger recorded albedo every 30 second during this period. Within a site I always tried to measure all three plots under the same sky conditions, to avoid potential differences emerging from the presence of clouds.

In my study, for the fixed sites, albedo was measured in 5 rounds, with approximately 4 weeks in between each round, except for the 5<sup>th</sup> round that was 2 weeks and a half apart from the 4<sup>th</sup> round due to logistic reasons. During the 1st round, only 2 of the 6 sites, and on the 2<sup>nd</sup> round only 4 of the 6 six sites were measured due to weather constraints. On the other three rounds I measured all fixed sites without disturbance. I added data from Vedin's (2016) study, who performed measurements in the same sites using the same methodology as I did in my study, to increase the sampling period. Vedin (2016) measured albedo between October 2016 and December 2016, and I performed my measurements between January 2017 and May 2017, to record the variation in albedo of the different vegetation types over time. Prior to the statistical analysis, January and February 2017 rounds had to be excluded since the number of sites measured was different from the other rounds. Similarly, Vedin's (2016) third measurement round was removed from the analysis, since site Nombali could not be measured due to the presence of two poached rhinos. Thus, I only used in the analysis the rounds where all the six sites were measured: October and November 2016, March, April and May 2017.

### *Vegetation measurements*

I recorded vegetation for each plot, using a point intercept method, where I laid out 2.6 m transects in the eight wind directions from the fixed middle point of each plot till the edges (Figure 4B). Every 20 centimeters along a transect I recorded species and, using a wooden stick with a centimeter scale, the maximum vegetation height of the vegetation and the number of times all living parts of each plant species touched the stick at that point (up to a maximum of 5 hits per species per point). The middle point was measured last and only on one of the eight

transects. With this design the central part of a plot is sampled more intensely compared to the rest, but this is compatible with the fact that the measurement taken by the albedometer is influenced the most by the vegetation directly underneath the sensor. In total, this gives 105 distinct points per plot.



*Figure 4.* A shows the albedometer on one of the plots; B represents a plot with the central point and the eight transects.

## 2.2.2 Study II: linking vegetation states and woody recruitment

To test if woody recruitment is more limited in grazing lawns than in tall bunch grassland, I walked an equal number of transects in grazing lawns and tall bunch grassland and recorded the number of woody plants of different height classes present in each vegetation type. The transects were walked both in Hluhluwe and Imfolozi (Figure 2) at the end of March 2017 and end of May 2017, respectively. Transects had a maximum length of 20 meters and I always paired a lawn transect with a tall bunch grass transect. When it was not possible to lay a 20 meters long transect, I would use the maximum length of the limiting vegetation type as transect length for both grassland types, i.e., if the maximum length for a grazing lawn transect possible in an area was 15 meters, then I would also limit



*Figure 5.* Biomass measurement on a transect using the DPM.

the tall bunch grass transect to 15 meters. Every meter along each transect, I recorded grass biomass using a Disc Pasture Meter (DPM) (Figure 5) and the predominant vegetation state under the disc ( $\geq 50\%$ ) was recorded according to one of the following four categories: maintained or unmaintained grazing lawn, forbs, or tall bunch grass. Subsequently, I walked the transect again and counted the number of woody plants per meter plot according to four different height classes:  $\leq 0.10$ ,  $\leq 0.50$ ,  $\leq 1.00$ , and  $> 1.00$  meters. A total number of 39 paired lawn-bunch grass transects was assessed, 20 in Hluhluwe and 19 in iMfolozi.

## 2.2 Statistical Analysis

Microsoft Excel 2010 was used to organize and process all the data before the analysis. All data was then analyzed using the software package R (version 3.3.3, R Core Team, 2017), together with the program RStudio (Version 1.0.153, RStudio Team, 2017). To build my models I used the package nlme (Pinheiro et al 2016).

### *Extra Sites Albedo Analysis*

For the extra sites, to test the effect of the different variables in albedo, I used a linear mixed-effects model with various fixed effects: vegetation type, time, percentage of woody plants cover, percentage of bare soil and vegetation height. I used two measurements of time: month and day of year (DOY). I used DOY as a covariate to test if there is a directional change in albedo over time, while I used month as an ordinal factor to test if there is any difference in albedo among months (directional or not), caused by random events such as rainfall. I decided to initially include both in my full model, but neither of these variables explained enough variation to end up in the final model. Due to the fact that my vegetation types were grouped within sites, I included site as a random effect to correct for this spatial autocorrelation. Although the residual variance and the variance for the random intercept were very small, and the estimates and p-values for the fixed effects did not change considerably when the random effect was removed (see Appendix II G), I decided to keep the random parameter in the final model to reflect my experimental design. The percentage of woody plants cover was calculated as the total number of vegetation hits divided by the number of woody plant's hits, per plot. Similarly, the percentage of bare soil was first calculated as the total number of vegetation hits divided by the number of bare soil hits, per plot, and then compared to the visually estimated percentage cover to obtain the

most accurate estimation for this parameter. Vegetation height was averaged per plot per site. In my final analysis, I added one measurement round of three of the fixed sites, with a strong contrast between vegetation types, to the 14 extra sites to increase the sample size: round 2 of 'Halfway', round 3 of 'Crossroads' and round 3 of 'AIPO'. To get to my final model, I simplified the full model by removing non-significant variables and testing with ANOVA whether the removal of variables was acceptable. My decisions were made based on the p-values of the different fixed effects and the Akaike Information Criterion (AIC) of the various models tested (see Appendix II A-I for details on model selection). I also tested for interactions between vegetation type and the following variables: woody plants cover, percentage of bare soil, vegetation height and DOY (see Appendix III).

#### *Fixed Sites Albedo Analysis*

Similarly to the extra sites analysis, to test the effect of the different variables in albedo on my fixed sites, I also used a linear mixed-effects model. However, to reflect the spatial dependency of my experimental design, I nested vegetation type within site as a random effect. I also added to the full model an interaction between the type of vegetation and month. I used the same procedure for model selection as for the extra sites (see Appendix IV A-H for details on model selection). I used simple linear regressions to test if albedo correlates with the number of bare soil, grass, woody plants and total vegetation hits.

#### *Woody Recruitment Analysis*

Since not all transects were of the same length, I calculated the density of woody plants per meter by dividing the number of woody plants individuals found by the full transect length. I did that for the four height classes separately. Similarly, I also calculated the percentage of lawn, bunch, forbs and bare soil per transect, since even grazing lawn transects had some tall grass patches and vice versa with tall grassland transects. To test for differences in woody recruitment between the different grassland types, I used linear mixed-effects models, with various fixed factors: grassland type, height class, area, DPM, percentage of lawn, percentage of tall bunch grass, percentage of forbs and percentage of bare soil. I added site as random factor to correct for the fact that transects were always paired. To answer the question whether the effect of grassland type depended on height class I also added an interaction between these two variables to my model. See Appendix V for model selection.





## 3. Results

### 3.1. Extra Sites

#### 3.1.1. Vegetation

Different vegetation types differed in canopy height, with vegetation in lawn plots being shorter than in tall grass plots, and woody plots (Figure 6A). Over time, the expected vegetation height pattern (lawn < tall < woody) was not always constant (Figure 6B). In March, tall bunch grass height surpassed woody plants plots' height.

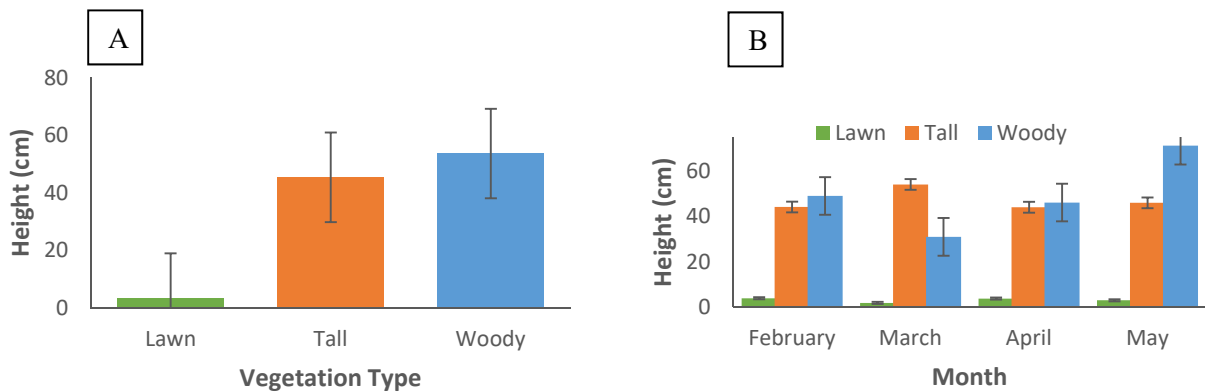


Figure 6. A represents the average vegetation height over each vegetation type over time; B represents the average vegetation height per plot over time.

#### 3.1.2. Albedo

Albedo differed among vegetation types ( $F_{2,32} = 8.0271$ ,  $p\text{-value} = 0.0015$ , Table 1, Figure 7). Bare soil, percentage of woody plants cover, DOY, month and vegetation height did not significantly influence albedo (Figure 8; Appendix II A-H). Albedo values varied between 0.1 and 0.20, except for the tall grass plot of the site Thyeni 1, which stands out as an outlier with an albedo value of 0.23 (Appendix I).

Table 1. Anova output of the final fitted linear mixed-effects model used to test the effect of vegetation type on albedo. Significant values are in bold.

|                    | numDF | denDF | F-value   | p-value          |
|--------------------|-------|-------|-----------|------------------|
| (Intercept)        | 1     | 32    | 1442.0135 | <b>&lt;.0001</b> |
| Type of Vegetation | 2     | 32    | 8.0271    | <b>0.0015</b>    |

Albedo of grazing lawn plots was higher than of woody encroached tall grassland plots (beta = -0.02235294, SD = 0.006528263, p-value = 0.0017), but did not differ between lawn and tall grassland plots (Table 2). To see if there was a difference between tall bunch grassland and woody encroached tall grassland plots, the same model was run changing the intercept to the tall grassland plots. The albedo of tall grassland plots was higher than that of woody encroached tall grassland plots (beta = -0.02294118, SD = 0.006528263, p-value = 0.0013).

Table 2. Summary table of the final fitted linear mixed-effects model used to test the effect of vegetation type on albedo. Intercept represents lawn vegetation. Significant values are in bold.

|                          | Value        | Std.Error   | DF | t-value   | p-value       |
|--------------------------|--------------|-------------|----|-----------|---------------|
| (Intercept)              | 0.17529412   | 0.004616179 | 32 | 37.97385  | <b>0.0000</b> |
| Type of Vegetation Tall  | 0.00058824   | 0.006528263 | 32 | 0.09011   | 0.9288        |
| Type of Vegetation Woody | - 0.02235294 | 0.006528263 | 32 | - 3.42403 | <b>0.0017</b> |

Table 3. Summary table of the final fitted linear mixed-effects model used to test the effect of vegetation type on albedo. Intercept represents tall grass vegetation. Significant values are in bold.

|                          | Value        | Std.Error   | DF | t-value   | p-value       |
|--------------------------|--------------|-------------|----|-----------|---------------|
| (Intercept)              | 0.17588235   | 0.004616179 | 32 | 38.10128  | <b>0.0000</b> |
| Type of Vegetation Lawn  | - 0.00058824 | 0.006528263 | 32 | - 0.09011 | 0.9288        |
| Type of Vegetation Woody | - 0.02294118 | 0.006528263 | 32 | - 3.51413 | <b>0.0013</b> |

No significant interactions were found between type of vegetation and percentage of woody plants cover ( $F_{2,29} = 0.4222$ , p-value = 0.6596), vegetation height ( $F_{2,29} = 0.20868$ , p-value = 0.8129), percentage of bare soil ( $F_{2,29} = 1.9454$ , p-value = 0.1611), month ( $F_{6,26} = 0.5400$ , p-value = 0.7729), or DOY ( $F_{2,30} = 1.24949$ , p-value = 0.3011) (see Appendix III A-E for detailed statistics). This indicates that there was little variation in the difference in albedo among the three vegetation types over time.

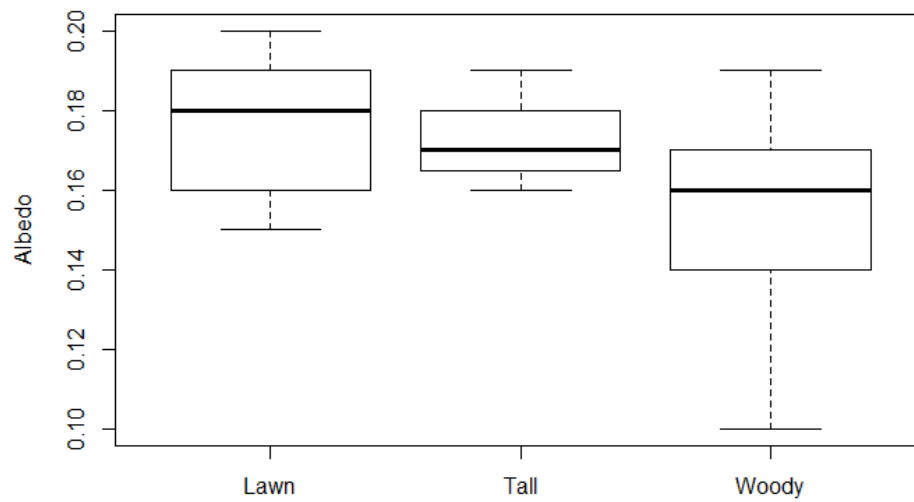
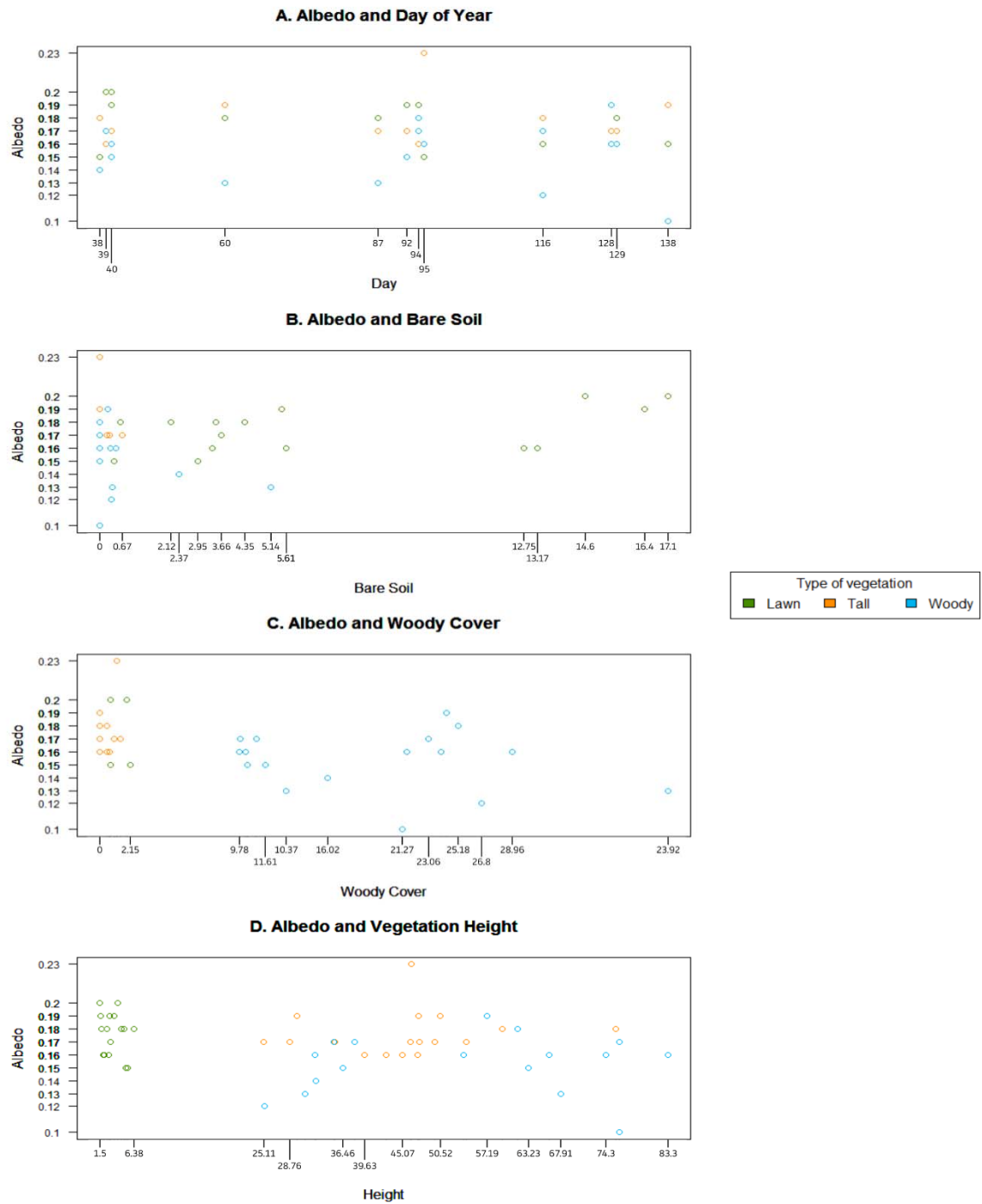


Figure 7. Mean albedo for the different vegetation types.



*Figure 8.* Graph A shows the albedo for every plot on each measurement day; B shows the relation between albedo and the percentage of bare soil, per plot; C shows the relation between albedo and the percentage of woody cover, per plot; D shows the relation between albedo and vegetation height, per plot.

## 3.2. Fixed Sites

### 3.2.1. Vegetation

Similarly to the extra sites, there was a difference in canopy height between the three types of vegetation (Figure 9A). During October and November, vegetation was much shorter for the three distinct types of vegetation studied, compared to March, April and May. After March, the average canopy height for each vegetation started to decrease (Figure 9B).

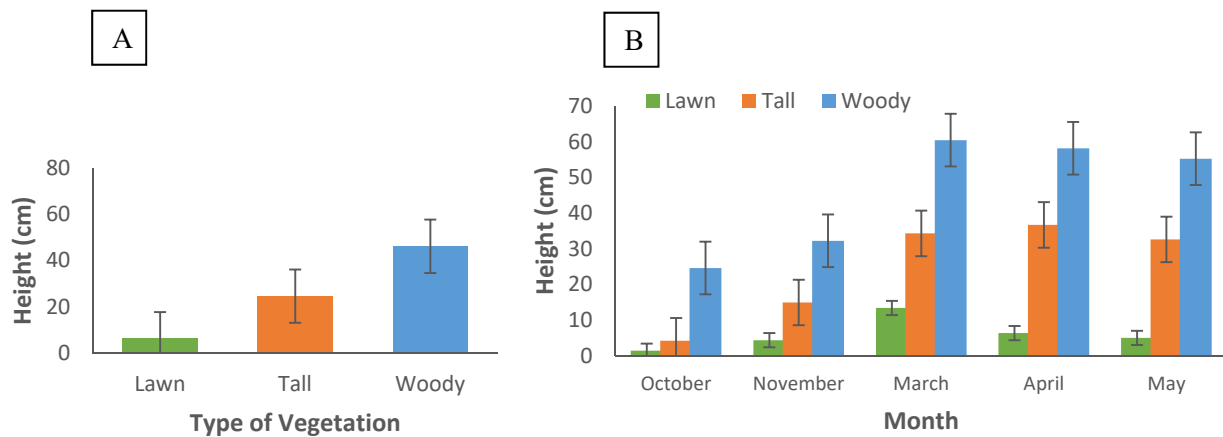


Figure 9. A represents the average vegetation height per plot over time; B represents the average vegetation height over each vegetation type over time.

### 3.2.2. Albedo

Woody plants cover did not affect albedo (Appendix IV for detailed statistics). Month and the type of vegetation, as well as the interaction between these two factors, did not have a significant effect on albedo, but were still kept in the final model (Table 4). The percentage of bare soil ( $F_{1,67} = 12.38513$ ,  $p\text{-value} = 0.0008$ ) and vegetation height ( $F_{1,67} = 6.92395$ ,  $p\text{-value} = 0.0105$ ) had a significant negative and positive effect on albedo, respectively (Table 4, Table 5).

Albedo values varied between 0.11 and 0.21, except for Nombali's first measurement of the lawn plot that produced a very low albedo value of 0.08 (Figure 10A). There was no significant difference in albedo between lawn and tall grass vegetation plots (Table 5), between lawn and woody vegetation plots (Table 5), or between tall and woody vegetation plots (Table 6). This is graphically shown in Figure 10B. Albedo values increased between October and November,

and November and March, but this trend was not followed during April and May measurement rounds (Figure 10C). During October and November, albedo was higher in lawn, followed by tall grass and then woody vegetation plots. March, April and May exhibited a slightly different pattern, with tall grass plots having higher albedo than lawn plots (Figure 10D). However, as stated above, month did not significantly influenced albedo.

Table 4. Anova output of the final fitted linear mixed-effects model. Significant values are in bold.

|                         | numDF | denDF | F-value   | p-value          |
|-------------------------|-------|-------|-----------|------------------|
| (Intercept)             | 1     | 67    | 274.99546 | <b>&lt;.0001</b> |
| Type of Vegetation      | 2     | 10    | 0.71467   | 0.5127           |
| Month                   | 1     | 67    | 3.80681   | 0.0552           |
| Bare Soil               | 1     | 67    | 12.38513  | <b>0.0008</b>    |
| Vegetation Height       | 1     | 67    | 6.92395   | <b>0.0105</b>    |
| Vegetation Type : Month | 2     | 67    | 2.00463   | 0.1427           |

Table 5. Summary table of the final fitted linear mixed-effects model. Intercept represents lawn vegetation. Significant values are in bold.

|                                  | Value        | Std. Error  | DF | t-value    | p-value       |
|----------------------------------|--------------|-------------|----|------------|---------------|
| (Intercept)                      | 0.15467857   | 0.009327546 | 67 | 16.582987  | <b>0.0000</b> |
| Type of Vegetation Tall          | - 0.00261908 | 0.010371466 | 10 | - 0.252528 | 0.8057        |
| Type of Vegetation Woody         | - 0.01323305 | 0.011630469 | 10 | - 1.137792 | 0.2817        |
| Month                            | 0.00406708   | 0.002084500 | 67 | 1.951106   | 0.0552        |
| Bare Soil                        | - 0.00077683 | 0.000220738 | 67 | - 3.519251 | <b>0.0008</b> |
| Vegetation Height                | 0.00044090   | 0.000167559 | 67 | 2.631340   | <b>0.0105</b> |
| Type of Vegetation Tall : Month  | - 0.00209088 | 0.002888166 | 67 | - 0.723947 | 0.4716        |
| Type of Vegetation Woody : Month | - 0.00576299 | 0.002962016 | 67 | - 1.945631 | 0.0559        |

Table 6. *Summary table of the final fitted linear mixed-effects model. Intercept represents tall grass vegetation. Significant values are in bold.*

|                                  | Value        | Std. Error  | DF | t-value    | p-value       |
|----------------------------------|--------------|-------------|----|------------|---------------|
| (Intercept)                      | 0.15205949   | 0.010469411 | 67 | 14.524168  | <b>0.0000</b> |
| Type of Vegetation Lawn          | 0.00261908   | 0.010371466 | 10 | 0.252528   | 0.8057        |
| Type of Vegetation Woody         | - 0.01061397 | 0.011042235 | 10 | - 0.961216 | 0.3591        |
| Month                            | 0.00197620   | 0.002450269 | 67 | 0.806524   | 0.4228        |
| Bare Soil                        | - 0.00077683 | 0.000220738 | 67 | - 3.519251 | <b>0.0008</b> |
| Vegetation Height                | 0.00044090   | 0.000167559 | 67 | 2.631340   | <b>0.0105</b> |
| Type of Vegetation Lawn : Month  | 0.00209088   | 0.002888166 | 67 | 0.723947   | 0.4716        |
| Type of Vegetation Woody : Month | - 0.00367211 | 0.002708378 | 67 | - 1.355834 | 0.1797        |

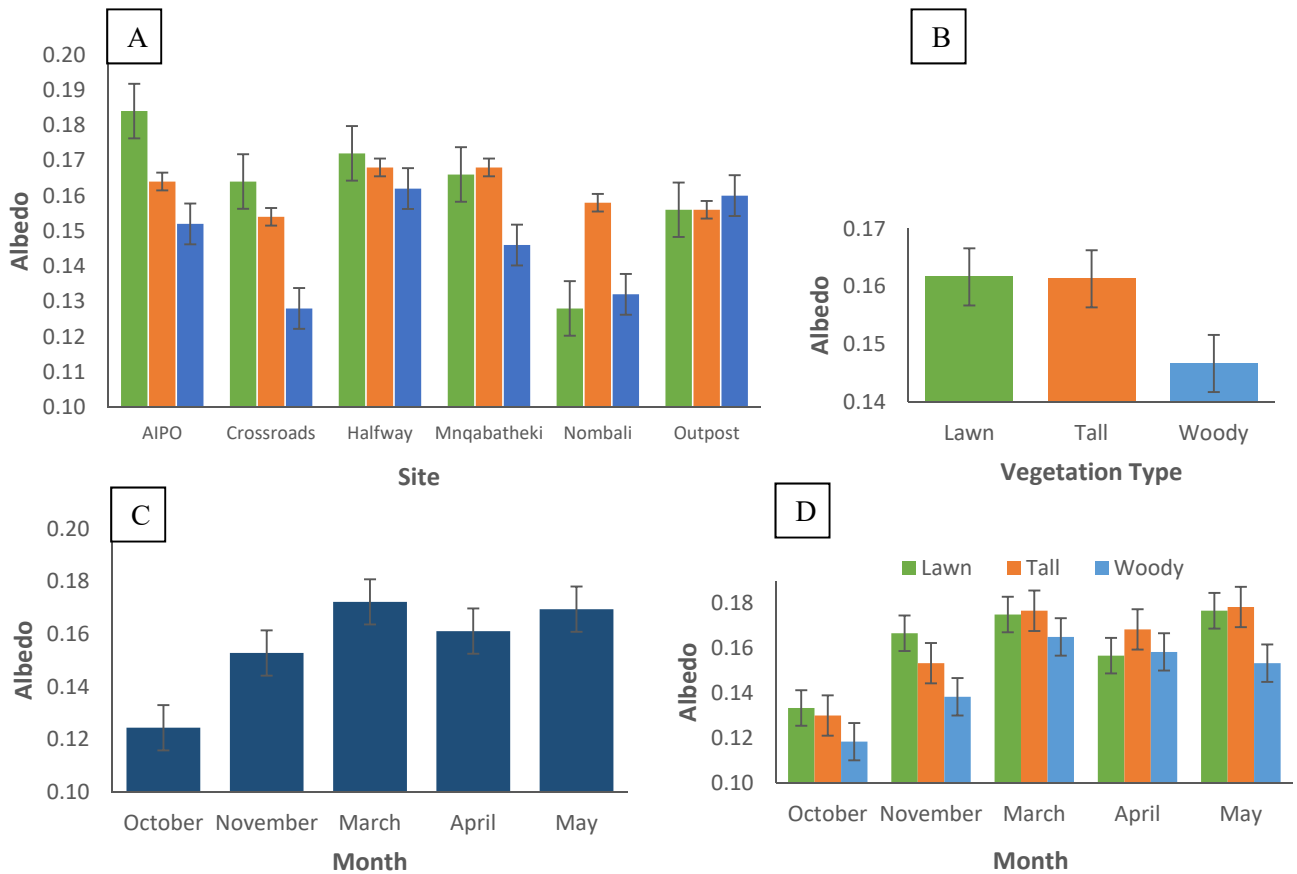


Figure 10. Graph A shows the mean albedo of all sites for the different vegetation types over time; B shows the mean albedo over vegetation type and time; C shows the mean albedo for the 5 measurement rounds; D shows the mean albedo for each vegetation type for each measurement round.

### 3.2.3. Vegetation – Albedo Interaction

The number of woody plants hits, similarly to the number of bare soil hits, had a negative correlation with albedo (Figure 11A and 11C). Albedo increased with the number of grass hits and the total number of vegetation hits (Figure 11B and 11D). Bare soil hits and grass hits explained much of the variability – approximately 49% and 42%, respectively. Table 7 summarizes the result of the regressions with the respective r-squared value. The number of hits was higher in March, April and May 2017, than in October and November 2016. Figure 12 presents an overview of these variables over time.



Table 7. Results from the regressions between albedo and bare soil, grass, woody plants and total vegetation hits. Significant values are in bold.

|                       | Intercept | Estimate    | T-value | p-value        | r <sup>2</sup> |
|-----------------------|-----------|-------------|---------|----------------|----------------|
| Bare soil Hits        | 0.1724875 | - 0.0012712 | - 9.15  | < <b>0.001</b> | 0.4875533      |
| Woody Plants Hits     | 0.1611    | - 0.0001645 | - 2.879 | <b>0.00501</b> | 0.0860596      |
| Grass Hits            | 0.1322    | 0.0001065   | 7.911   | < <b>0.001</b> | 0.4155996      |
| Total Vegetation Hits | 0.1309    | 0.00009158  | 6.008   | < <b>0.001</b> | 0.2908506      |

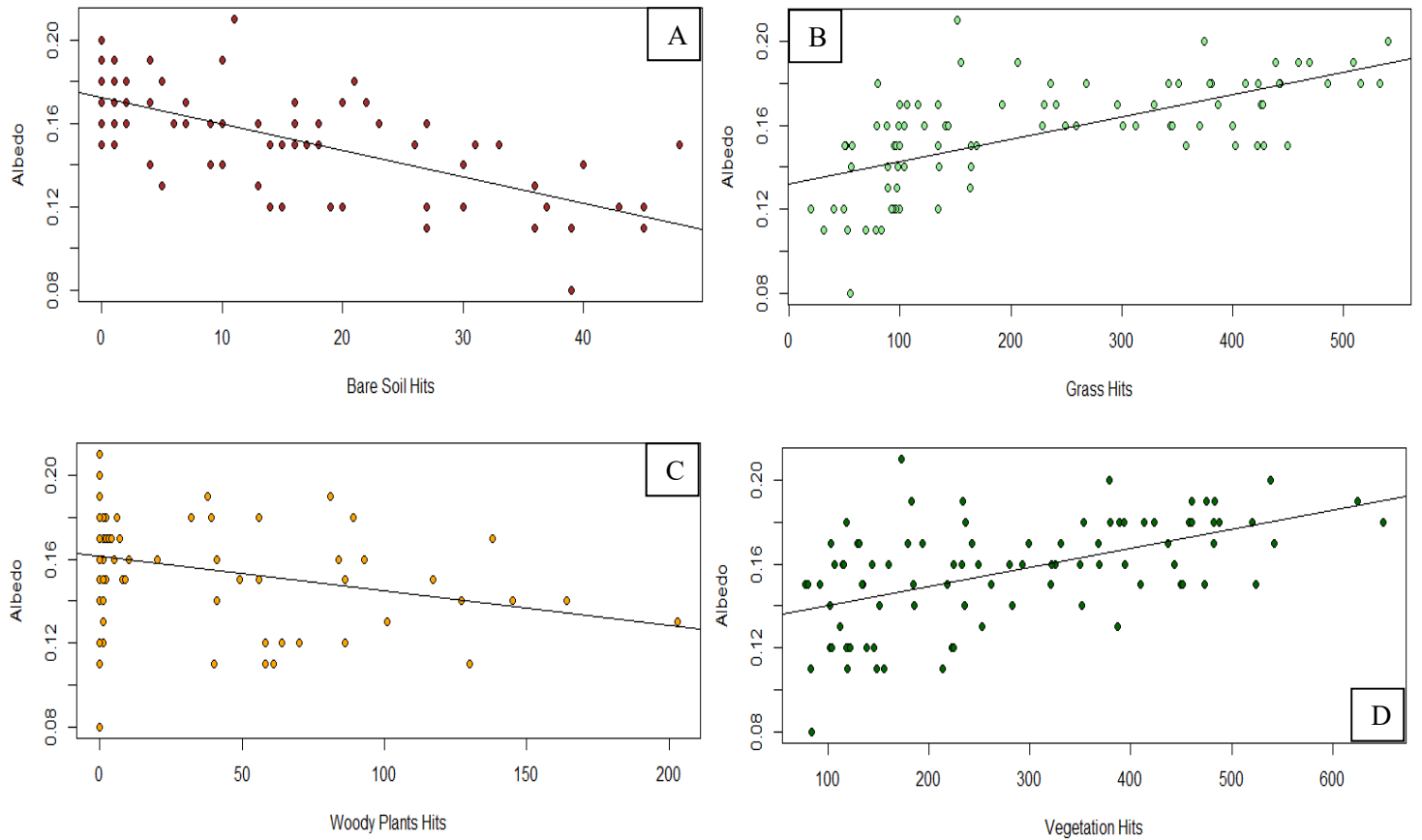
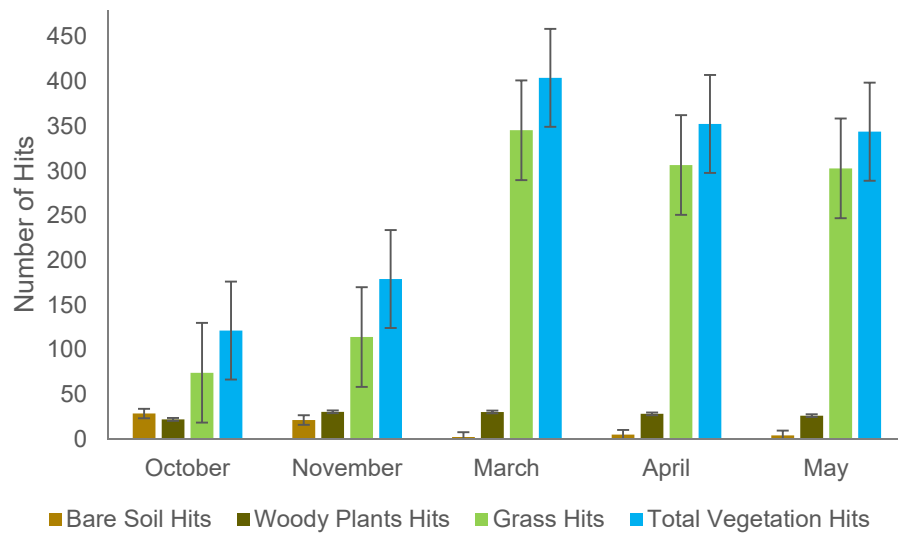


Figure 11. Graph A shows the correlation between albedo and number of bare soil hits, B the correlation between albedo and number of grass hits, C the correlation between albedo and woody



plants hits, and D the correlation between albedo and the total number of vegetation hits. Ablines are also represented.

Figure 12. Bare soil, woody plants, grass and total vegetation hits over time.

### 3.3. Woody Recruitment

There was a significant difference between grassland types ( $F_{1,266} = 19.05821$ ,  $p$ -value =  $<.0001$ , Table 8), with a higher prevalence of woody plants in bunch grass transects (Figure 13A). Woody plants height ( $F_{3,266} = 12.66983$ ,  $p$ -value =  $<.0001$ ) negatively influenced the number of woody plants (Table 8), with number of woody plants decreasing as height increased (Figure 13B). The interaction between grassland type and woody plants' height ( $F_{3,266} = 2.80177$ ,  $p$ -value =  $0.0404$ , Table 8) was also significant, indicating that grassland type negatively interacted with the height of woody plants individuals (Table 9, Table 10).

Table 8. Anova output of the final fitted linear mixed-effects model used to test the effect of grassland type and height class on the number of woody plants. Intercept represents bunch grassland. Significant values are in bold.

|                | numDF | denDF | F-value  | p-value          |
|----------------|-------|-------|----------|------------------|
| (Intercept)    | 1     | 266   | 50.34482 | <b>&lt;.0001</b> |
| Grassland Type | 1     | 266   | 19.05821 | <b>&lt;.0001</b> |
| Height Class   | 3     | 266   | 12.66983 | <b>&lt;.0001</b> |

|                               |   |     |         |               |
|-------------------------------|---|-----|---------|---------------|
| Grassland Type : Height Class | 3 | 266 | 2.80177 | <b>0.0404</b> |
|-------------------------------|---|-----|---------|---------------|

The height classes  $\leq 0.10$  cm,  $\leq 0.50$  cm and  $\leq 100$  cm were significant for the bunch grass type of vegetation (Table 9), but not for lawn grassland (Table 10). The difference between grassland type was more notorious in Hluhluwe than iMfolozi (Figure 13C), but still it was not significant (see Appendix V for detailed statistics). No woody plants higher than 1 m were found in lawn transects, and the majority of woody individuals in both type of transect belonged to the class height between 10 and 50 cm (Figure 13B).

Table 9. Summary table of the final fitted linear mixed-effects model used to test the effect of grassland type and height class on the number of woody plants. Intercept represents bunch grassland. Significant values are in bold.

|                                   | Value        | Std. Error | DF  | t-value    | p-value       |
|-----------------------------------|--------------|------------|-----|------------|---------------|
| (Intercept)                       | 0.13538462   | 0.01908060 | 266 | 7.095408   | <b>0.0000</b> |
| Grassland.TypeLawn                | - 0.09461538 | 0.02167308 | 266 | - 4.365571 | <b>0.0000</b> |
| Height.Class.L ( $\leq 0.10$ cm)  | - 0.11123005 | 0.03065037 | 266 | - 3.628996 | <b>0.0003</b> |
| Height.Class.Q ( $\leq 0.50$ cm)  | - 0.11948718 | 0.03065037 | 266 | - 3.898393 | <b>0.0001</b> |
| Height.Class.C ( $\leq 100$ cm)   | 0.09517623   | 0.03065037 | 266 | 3.105223   | <b>0.0021</b> |
| Grassland.TypeLawn:Height.Class.L | 0.05962848   | 0.04334617 | 266 | 1.375634   | 0.1701        |
| Grassland.TypeLawn:Height.Class.Q | 0.09205128   | 0.04334617 | 266 | 2.123632   | <b>0.0346</b> |
| Grassland.TypeLawn:Height.Class.C | - 0.06134853 | 0.04334617 | 266 | - 1.415316 | 0.1581        |

Table 10. Summary table of the final fitted linear mixed-effects model used to test the effect of grassland type and height class on the number of woody plants. Intercept represents lawn grassland. Significant values are in bold.

|                                   | Value       | Std. Error | DF  | t-value   | p-value       |
|-----------------------------------|-------------|------------|-----|-----------|---------------|
| (Intercept)                       | 0.04076923  | 0.01908059 | 266 | 2.136686  | <b>0.0335</b> |
| Grassland.TypeBunch               | 0.09461538  | 0.02167308 | 266 | 4.365571  | <b>0.0000</b> |
| Height.Class.L ( $\leq 0.10$ cm)  | -0.05160157 | 0.03065037 | 266 | -1.683555 | 0.0934        |
| Height.Class.Q ( $\leq 0.50$ cm)  | -0.02743590 | 0.03065037 | 266 | -0.895125 | 0.3715        |
| Height.Class.C ( $\leq 100$ cm)   | 0.03382770  | 0.03065037 | 266 | 1.103664  | 0.2707        |
| Grassland.TypeLawn:Height.Class.L | -0.05962848 | 0.04334617 | 266 | -1.375634 | 0.1701        |

|                                   |             |            |     |           |               |
|-----------------------------------|-------------|------------|-----|-----------|---------------|
| Grassland.TypeLawn:Height.Class.Q | -0.09205128 | 0.04334617 | 266 | -2.123631 | <b>0.0346</b> |
| Grassland.TypeLawn:Height.Class.C | 0.06134853  | 0.04334617 | 266 | 1.415316  | 0.1581        |

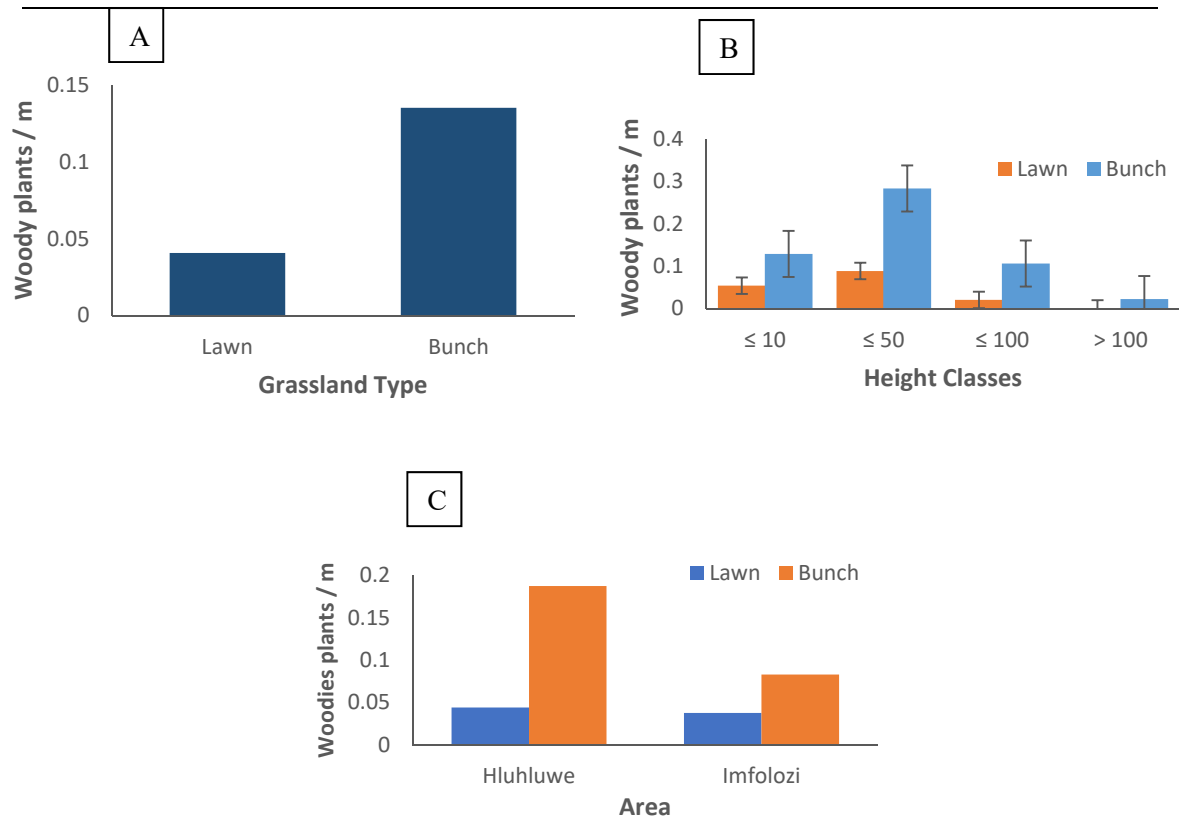


Figure 13. Graph A shows how the number of woody plants varied between the two grassland types; B exposes the differences in the number of woody plants between different height classes, both for lawn and bunch grass transects.; C shows the variation in woody plants between Hluhluwe and Imfolozi, both for lawn and bunch grass transects.

## 4. Discussion

Most of the studies that have been done on albedo were from the boreal and temperate zone (Beringer et al., 2005, Chapin Iii et al., 2000, Euskirchen et al., 2007, Williamson et al., 2016, Juszak et al., 2014), with fewer studies in the tropical and sub-tropical zones (Allen et al., 1994, Syktus and McAlpine, 2016, Knorr and Schnitzler, 2006). When talking about studies that specifically approach the interaction between grazing and albedo the focus on high latitudes is even more obvious (Cohen et al., 2013, te Beest et al., 2016, Vowles et al., 2017). Thus, more studies that better explore the extent of grazing influence in sub-tropical regions are needed. The present study intended to investigate the influence of the different vegetation states on the local albedo of Hluhluwe-iMfolozi Park, which indirectly addresses this gap. As hypothesized, I found that different vegetation types differ in albedo, with grazing lawns having a significantly higher albedo than woody encroached tall grassland plots (Table 2). I showed that tall bunch grass have a significantly higher albedo than woody encroached tall grass, but, contrary to my prediction, do not significantly differ from grazing lawns plots (Table 3). I also found that grazing lawns seem to condition woody encroachment over the landscape, being less prone to it than tall bunch grass (Table 8, Figure 13A). As expected, albedo was negatively correlated with the amount of bare soil, probably due to the dark soil coloration. Contrary to what was expected, the regression between albedo and the amount of woody plants individuals was negative. On the other hand, albedo increased with more grass and more vegetation hits (Table 7). Comparing the albedo of all the plots included in this study (both from fixed and extra sites), lawn had 0.00084 higher albedo than tall grassland, and 0.01797 higher albedo than woody plants plots, while tall grassland had 0.01713 higher albedo than woody encroached plots. These differences in albedo between vegetation types may not seem large, but Cohen et al. (2013) showed that even small differences are able to impact climate locally – a variation between 0 and 0.05 in mean albedo led to a higher solar energy absorption that contributed up to 0.46 W/m<sup>2</sup> to the energy balance of the year. However, these findings cannot be directly extrapolated to my study, since biochemical and biophysical effects can be significantly different according to latitude, meaning that smaller differences in albedo in a higher latitude might be sufficient to alter local climate, but the same differences might not be as relevant in tropical and sub-tropical regions. In fact, Bala et al. (2007) suggested that the effect of albedo is greater in the Northern Hemisphere mid-latitudes and high latitudes, while the effect of transpiration and carbon feedbacks are more relevant in the tropics. Several authors argue that tropical deforestation would lead to an increase in surface temperature and

decrease in annual rainfall and evapotranspiration (Foley et al., 2003, Bonan, 2008, Bala et al., 2007). Syktus and McAlpine (2016), using climate models to assess the effects of restoration of savanna woodlands in Australia, showed that the warming effect due to the reduced woodland albedo was offset by the cooling effect of evapotranspiration. This indicates that evapotranspiration might also play a key role in African savannas. Thus, further studies that investigate its effect for different vegetation types – particularly differences between grazing lawns, bunch tall grassland and woody encroached tall grassland – are needed to better comprehend the interaction between albedo and evapotranspiration in sub-tropical regions.

When the fixed sites used on this study were set in October 2016 by Vedin (2016), the area had been through a severe drought, and the contrast between vegetation types was not always evident. Despite this, Vedin (2016) found clear differences in albedo between the three types of vegetation, and further hypothesized that those differences would be greater if the plots had been more representative to begin with. By adding representative extra sites to my study, I intended to corroborate the differences between vegetation types - I found that the three vegetation types did indeed differ in albedo (Figure 7), but only the difference between lawn and woody encroached tall grassland (Table 2), and the difference between tall bunch grass and woody encroached tall grassland plots were significant, while lawn and tall bunch grass plots were not significantly different (Table 3). Also, from the analysis of the extra sites, the percentage of bare soil, the percentage of woody cover, the time and the vegetation height did not seem to influence albedo (Figure 8), which is somehow unexpected.

The two factors that significantly affected the albedo on the long-term sites of this study were the percentage of bare soil and the vegetation height (Table 4). Vegetation was much shorter in October and November than in March, April and May (Figure 9B), which could be explained by the severe drought the area was going through during that period (Vedin, 2016). After March, the vegetation height slightly started to decrease on the three vegetation types, which coincides with the end of the growing season. In March, the average height for the tall grassland plots was higher than for woody encroached tall grassland plots, which might be a result of the heavy rainfall during February (personal observation). These shifts in vegetation height are relevant, since my results from the fixed sites analysis show vegetation height influences albedo. In fact, albedo increased between October and March, which corresponds to the growing season, and started to decrease after that. During the October and November measurement rounds, albedo was higher in grazing lawns, followed by tall grassland and then woody encroached grassland, but this distinct pattern was not maintained through the remaining measurement rounds. In March, April and May, tall bunch grassland plots had slightly higher

albedo than grazing lawns plots. This could be because it was also during that period that the vegetation height shift occurred - which again might be the result of the heavy rainfall during previous months. Nonetheless, these differences were small, and, according to my model, month did not explain much of the variation in albedo. Possible explanations for why vegetation height had a different effect on albedo between fixed and extra sites might be due to sample size – the number of fixed sites was smaller than the number of the extra sites - and to plot vegetation composition - since extra sites, contrary to the fixed sites, always had a clear contrast between vegetation types. Vedin (2016), using the same plots, found a significant difference in albedo between vegetation types. However, in my data collected from March to May 2017 I did not find any significant differences. The differences might be related to differences in plot vegetation composition, since the sites changed dramatically between the two studies. In 2016, the height difference between vegetation types was little. Between November 2016 and March 2017, the average number of vegetation hits more than doubled (Figure 12), and the height difference between vegetation types was much more obvious in 2017's measurements than in 2016 (Figure 9B), showing that vegetation was much taller and denser. Even during the period of my study, vegetation across HiP changed considerably (personal observation), indicating that month should indeed be an important factor when explaining albedo variation. Perhaps increasing the measurement period and assessing albedo over an entire year would produce clear results regarding the role of month. Another factor that could explain differences between Vedin (2016) and my study is the height on which the albedometer was positioned, which was standardized for both studies. However, vegetation height dramatically increased from one study to the other, resulting that in some of my sites the albedometer sensor was placed below the vegetation line.

In my study, albedo and bare soil were negatively correlated (Figure 11A). This is contrary to the results found in other studies. Knorr and Schnitzler (2006) showed that desert areas in the Sahara had very high albedo values. A possible explanation for my findings might be the soil colour on the plots, since some of the sites had a relatively dark bare soil compared with the surrounding vegetation. Furthermore, soil moisture content seemed to impact soil colour (personal observation), resulting in darker soils after rain. Although I tried to avoid it as much as possible, I often performed albedo measurements on days after it had been raining, resulting in darker soil, which would negatively influence albedo. Bare soil decreased over time, being at its minimum in March, when albedo values were also at its highest. This could suggest that bare soil was the main driver of albedo variation in this study. However, these changes might also just be a consequence of the growing season, since it has been shown before that albedo increases during the growing season (Williamson et al., 2016). Juszak et al. (2014) proposed that this happens

due to the higher leaf to branch ratio – leaf area index is likely to increase over the growing season, reflecting more radiation than branches – that leads to albedo increase.

According to several studies, more complex surfaces, such as tree canopies, are able to trap more radiation, leading to decreases in albedo (A Coakley, 2003, Beringer et al., 2005). Thus, I expected that the number of vegetation hits would negatively correlate with albedo. However, the linear regression showed the opposite (Figure 11D), and I think this could be explained by soil coloration once more. Bare soil had low albedo values (Vedin, 2016, personal observation, 2017), thus increases in vegetation hits resulted most likely in a higher albedo, since grass would have higher albedo than bare soil. Moreover, in some of my plots, the grass was flowering, and inflorescences' structure is unlikely to reflect light the same way as for instance branches and leaves. The presence of inflorescences also made the plots lighter, which probably increased albedo. Thus, the number of hits might not always be a good indicator of surface complexity. Furthermore, the fact that I would only count five hits as the maximum number of vegetation hits per point, can be sometimes under representative of the actual vegetation structure and composition. Another explanation could be that vegetation development created a homogeneous surface, efficient in reflecting radiation, increasing albedo (Williamson et al., 2016). However, since the linear regression reflected the interaction between albedo and vegetation hits from all the different plots, I think this explanation might not be applicable to this case. Surprisingly, contrary to what I was expecting, the percentage of woody plants cover did not influence albedo in the model and the linear regression confirmed the low correlation between these two variables (Figure 11C). A possible explanation is that grass was present in all plots, while the presence of woody plants was mostly confined to woody encroached tall grassland plots, which unbalances the correlation (Vedin, 2016).

My results support that the existence of grazing lawn patches can influence albedo of savanna's landscapes. As mentioned before, grazers are known for their capacity of shaping vegetation cover, by inducing vegetation states shifts. Megaherbivores can have a greater impact on these vegetation shifts than smaller herbivores (Owen-Smith, 1987), since their body size decreases risk of predation. The decline of mammoth populations during the Pleistocene has been associated with profound changes in vegetation cover that led to a reduction in albedo (Doughty et al., 2010). The existent literature on the impact of megaherbivores on vegetation has mainly focused on browsers, such as the elephant (Asner et al., 2016, Kerley et al., 2008). However, Boundja and Midgley (2010) found that elephants avoid the tree species associated with bush encroachment. On the other hand, megagrazers, such as white rhino, with their capacity of creating grazing lawns (Waldram et al., 2008), might be of particular relevance, since I showed that this type of vegetation



has a higher albedo. White rhinos are then able to influence the overall albedo of the landscape, keeping it higher and, consequently, reducing the temperature locally. Nonetheless, the role of smaller grazers on grazing lawns' dynamic should not be underestimated. A study by Cromsigt and Olff (2008) suggested that megaherbivores might be the ones initiating the lawn formation process, but smaller species, such as impala and warthog, contribute to the maintenance of the lawn by keeping it short and more prone to lawn species colonization. Furthermore, my results suggest that grazing lawns are less prone to woody encroachment compared to tall bunch grass. In Hluhluwe I found a slightly higher number of woody plants individuals on bunch transects compared to Imfolozi. This might be the result of the different rainfall patterns, with grass recovering time being shorter in Hluhluwe due to the higher precipitation rates (Balfour and Howison, 2002). No woody plants higher than one meter were recorded in lawn transects, which might be a consequence of grazing pressure. Similarly to other studies (te Beest et al., 2016, Olofsson et al., 2009), these results are an important indicator of the interaction between grazers and albedo – short grazed grass has higher albedo, and by further maintaining grass short, grazers prevent woody invasion, keeping albedo high, and consequently cooling the surface. Thus, my study supports that, as previously argued by te Beest et al. (2016) te Beest et al. (2016), herbivore management could be used to mitigate climate warming.

This study is of particular importance in light of the recent rhino poaching crisis in South Africa. Poaching events increased exponentially in Kruger National Park since the year 2006, with 252 white rhinos being poached in 2011 (Ferreira et al., 2012). According to Büscher (2016), more than a thousand rhinos have been poached every year since 2013. Maintaining these rates, wild white rhino populations will disappear in the next 20 years (Ferreira et al., 2012). Despite the clear negative effects, the cost of removing a large apex consumer such as a megaherbivore from nature - phenomena known as trophic downgrading (Estes et al., 2011) - is still lacking empirical evidence. Poaching might not only be affecting the rhino population numbers, but indirectly affecting ecosystems and contributing to climate changes. Hence, more studies like the present are needed to shed a bit more light into this subject, focusing on the possible loss of the white rhino in a savanna ecosystem.

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## References

- A COAKLEY, J. 2003. *Reflectance and albedo, surface*.
- ALKAMA, R. & CESCATTI, A. 2016. Biophysical climate impacts of recent changes in global forest cover. *Science*, 351, 600-604.
- ALLEN, S., WALLACE, J., GASH, J. & SIVAKUMAR, M. 1994. Measurements of albedo variation over natural vegetation in the Sahel. *International Journal of Climatology*, 14, 625-636.
- ARCHIBALD, S., BOND, W., STOCK, W. & FAIRBANKS, D. 2005. Shaping the landscape: fire–grazer interactions in an African savanna. *Ecological applications*, 15, 96-109.
- ASNER, G. P., VAUGHN, N., SMIT, I. P. J. & LEVICK, S. 2016. Ecosystem-scale effects of megafauna in African savannas. *Ecography*, 39, 240-252.
- BALA, G., CALDEIRA, K., WICKETT, M., PHILLIPS, T. J., LOBELL, D. B., DELIRE, C. & MIRIN, A. 2007. Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences*, 104, 6550-6555.
- BALFOUR, D. & HOWISON, O. 2002. Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. *African Journal of Range and Forage Science*, 19, 45-53.
- BERINGER, J., CHAPIN, F. S., THOMPSON, C. C. & MCGUIRE, A. D. 2005. Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, 131, 143-161.
- BETTS, R. A. 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. *Nature*, 408, 187-190.
- BONAN, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *science*, 320, 1444-1449.
- BOUNDJA, R. P. & MIDGLEY, J. J. 2010. Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa. *African Journal of Ecology*, 48, 206-214.
- BROOKS, P. & MACDONALD, I. 1983. An ecological case history of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex, Natal, South Africa. *Management of large mammals in African conservation areas*, 51-77.
- CHAPIN, F. S., RANDERSON, J. T., MCGUIRE, A. D., FOLEY, J. A. & FIELD, C. B. 2008. Changing feedbacks in the climate–biosphere system. *Frontiers in Ecology and the Environment*, 6, 313-320.
- CHAPIN III, F. S., EUGSTER, W., P. MCFADDEN, J., LYNCH, A. & WALKER, D. 2000. *Summer Differences among Arctic Ecosystems in Regional Climate Forcing*.
- COHEN, J., PULLIAINEN, J., MÈNARD, C. B., JOHANSEN, B., OKSANEN, L., LUOJUS, K. & IKONEN, J. 2013. Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of Environment*, 135, 107-117.
- CROMSIGT, J. P., ARCHIBALD, S. & OWEN-SMITH, N. 2017. *Conserving Africa's mega-diversity in the Anthropocene: The Hluhluwe-iMfolozi Park story*, Cambridge University Press.
- CROMSIGT, J. P. & KUIJPER, D. P. 2011. Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores? *Perspectives in Plant Ecology, Evolution and Systematics*, 13, 207-215.
- CROMSIGT, J. P. & OLFF, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, 87, 1532-1541.
- CROMSIGT, J. P. & OLFF, H. 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. *Oikos*, 117, 1444-1452.
- CROMSIGT, J. P. & TE BEEST, M. 2014. Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *Journal of Ecology*, 102, 566-575.
- CROMSIGT, J. P. G. M. 2006. Large herbivores in space: Resource partitioning among savanna grazers in a heterogeneous environment. *Links*, 11, 01.

- DOUGHTY, C. E., WOLF, A. & FIELD, C. B. 2010. Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming? *Geophysical Research Letters*, 37.
- ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D. & JACKSON, J. B. 2011. Trophic downgrading of planet Earth. *science*, 333, 301-306.
- EUSKIRCHEN, E. S., MCGUIRE, A. D. & CHAPIN, F. S. 2007. Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming. *Global Change Biology*, 13, 2425-2438.
- FERREIRA, S. M., BOTHA, J. M. & EMMETT, M. C. 2012. Anthropogenic influences on conservation values of white rhinoceros. *PLoS One*, 7, e45989.
- FOLEY, J. A., COSTA, M. H., DELIRE, C., RAMANKUTTY, N. & SNYDER, P. 2003. Green surprise? How terrestrial ecosystems could affect earth's climate. *Frontiers in Ecology and the Environment*, 1, 38-44.
- HEMPSON, G. P., ARCHIBALD, S., BOND, W. J., ELLIS, R. P., GRANT, C. C., KRUGER, F. J., KRUGER, L. M., MOXLEY, C., OWEN-SMITH, N. & PEEL, M. J. 2015. Ecology of grazing lawns in Africa. *Biological Reviews*, 90, 979-994.
- HOFFMANN, W. A. & JACKSON, R. B. 2000. Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate*, 13, 1593-1602.
- JUSZAK, I., ERB, A. M., MAXIMOV, T. C. & SCHAEPMAN-STRUB, G. 2014. Arctic shrub effects on NDVI, summer albedo and soil shading. *Remote Sensing of Environment*, 153, 79-89.
- KERLEY, G. I., LANDMAN, M., KRUGER, L., OWEN-SMITH, N., BALFOUR, D., DE BOER, W., GAYLARD, A., LINDSAY, K. & SLOTOW, R. 2008. Effects of elephants on ecosystems and biodiversity.
- KNORR, W. & SCHNITZLER, K.-G. 2006. Enhanced albedo feedback in North Africa from possible combined vegetation and soil-formation processes. *Climate Dynamics*, 26, 55-63.
- LE ROUX, E., CLINNING, G., DRUCE, D. J., OWEN-SMITH, N., GRAF, J. & CROMSIGT, J. P. 2017. 4 r Temporal Changes in the Large Herbivore Fauna of Hluhluwe-iMfolozi Park. *Conserving Africa's mega-diversity in the Anthropocene: The Hluhluwe-iMfolozi Park story*, 80.
- LINKLATER, W. L. & HUTCHESON, I. R. 2010. Black rhinoceros are slow to colonize a harvested neighbour's range. *South African Journal of Wildlife Research*, 40, 58-63.
- MCNAUGHTON, S. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, 863-886.
- NAUDTS, K., CHEN, Y., MCGRATH, M. J., RYDER, J., VALADE, A., OTTO, J. & LUYSSAERT, S. 2016. Europe's forest management did not mitigate climate warming. *Science*, 351, 597-600.
- OLOFSSON, J., OKSANEN, L., CALLAGHAN, T., HULME, P. E., OKSANEN, T. & SUOMINEN, O. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15, 2681-2693.
- OWEN-SMITH, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 351-362.
- OWEN-SMITH, N. 2004. Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, 19, 761-771.
- OWEN-SMITH, R. N. 1988. *Megaherbivores: the influence of very large body size on ecology*, Cambridge university press.
- PAINE, R. T. 1995. A conversation on refining the concept of keystone species. JSTOR.
- STEVENS, N., LEHMANN, C. E., MURPHY, B. P. & DURIGAN, G. 2017. Savanna woody encroachment is widespread across three continents. *Global change biology*, 23, 235-244.
- SYKTUS, J. I. & MCALPINE, C. A. 2016. More than carbon sequestration: Biophysical climate benefits of restored savanna woodlands. *Scientific Reports*, 6.
- TE BEEST, M., SITTERS, J., MÉNARD, C. B. & OLOFSSON, J. 2016. Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environmental Research Letters*, 11, 125013.
- VAN DER WAAL, C., KOOL, A., MEIJER, S. S., KOHI, E., HEITKÖNIG, I. M., DE BOER, W. F., VAN LANGEVELDE, F., GRANT, R. C., PEEL, M. J. & SLOTOW, R. 2011. Large

- herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia*, 165, 1095-1107.
- VOWLES, T., LOVEHAY, C., MOLAU, U. & BJÖRK, R. G. 2017. Contrasting impacts of reindeer grazing in two tundra grasslands. *Environmental Research Letters*, 12, 034018.
- WALDRAM, M. S., BOND, W. J. & STOCK, W. D. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*, 11, 101-112.
- WHATELEY, A. & PORTER, R. 1983. The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi game reserve complex. *Bothalia*, 14, 745-758.
- WILLIAMSON, S. N., BARRIO, I. C., HIK, D. S. & GAMON, J. A. 2016. Phenology and species determine growing-season albedo increase at the altitudinal limit of shrub growth in the sub-Arctic. *Global change biology*.

# Appendix

## I. Figures

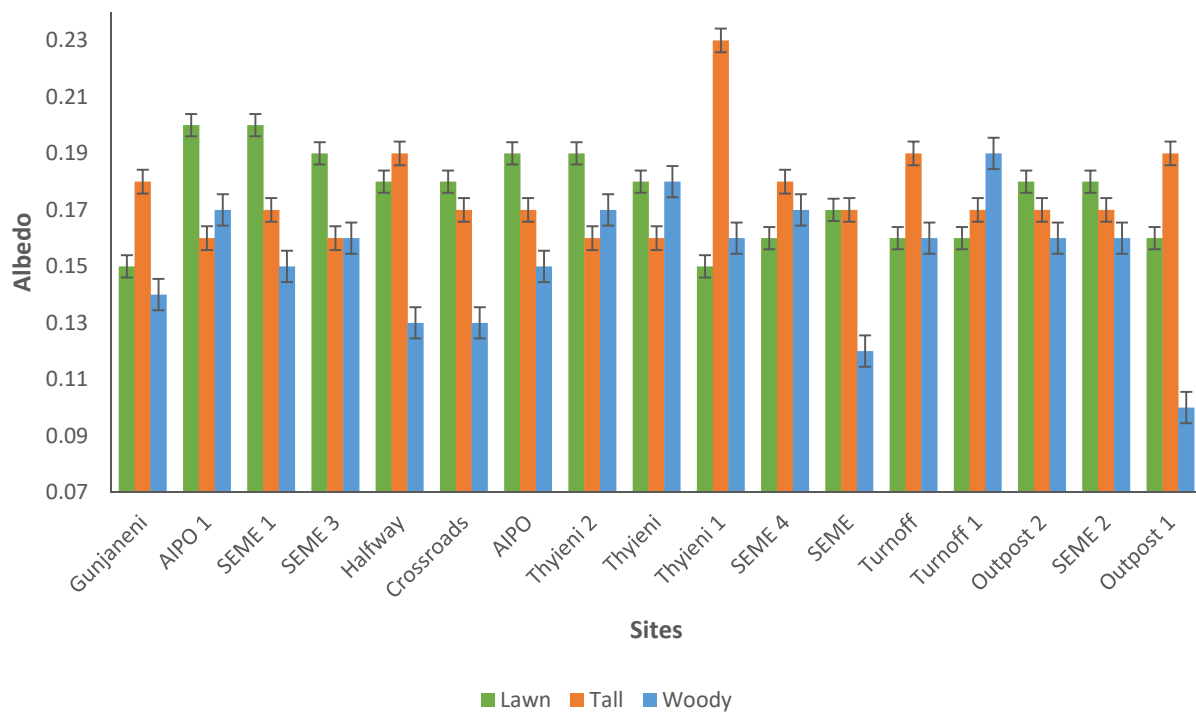


Figure 1. Albedo for the Extra Sites (plus 3 Fixed Sites)

## II. Extra Sites (plus 3 Fixed Sites) Model Simplification

Table A. Anova output of the fitted linear mixed-effects model with vegetation type, day of year, month, woody plants cover, bare soil and vegetation height as fixed effects and site as random effect. *lme(Albedo ~ Type of Vegetation + Day of Year + Month + Woody Plants Cover + Bare Soil + Vegetation Height, random=~1|Site, method="ML")*

| Model 1            | numDF | denDF | F-value  | p-value |
|--------------------|-------|-------|----------|---------|
| (Intercept)        | 1     | 29    | 44.39126 | <.0001  |
| Type of Vegetation | 2     | 29    | 1.18768  | 0.3193  |
| Day of Year        | 1     | 12    | 2.05314  | 0.1774  |
| Month              | 3     | 12    | 0.89782  | 0.4706  |
| Woody Plants Cover | 1     | 29    | 0.02610  | 0.8728  |
| Bare Soil          | 1     | 29    | 0.91136  | 0.3476  |
| Vegetation Height  | 1     | 29    | 0.37874  | 0.5431  |

Table B. Anova output of the fitted linear mixed-effects model without woody plants cover. *lme(Albedo ~ Type of Vegetation + Day of Year + Month + Bare Soil + Vegetation Height, random=~1|Site, method="ML")*

| Model 2            | numDF | denDF | F-value  | p-value |
|--------------------|-------|-------|----------|---------|
| (Intercept)        | 1     | 30    | 46.05129 | <.0001  |
| Type of Vegetation | 2     | 30    | 6.41033  | 0.0048  |
| Day of Year        | 1     | 12    | 2.18755  | 0.1649  |
| Month              | 3     | 12    | 1.01011  | 0.4221  |
| Bare Soil          | 1     | 30    | 0.90763  | 0.3484  |
| Vegetation Height  | 1     | 30    | 0.52267  | 0.4753  |

Table C. Anova output of the fitted linear mixed-effects model without vegetation height. *lme(Albedo ~ Type of Vegetation + Day of Year + Month + Bare Soil, random=~1|Site, method="ML")*

| <b>Model 3</b>     | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|--------------------|--------------|--------------|----------------|----------------|
| (Intercept)        | 1            | 31           | 47.45455       | <.0001         |
| Type of Vegetation | 2            | 31           | 6.68129        | 0.0039         |
| Day of Year        | 1            | 12           | 2.28238        | 0.1567         |
| Month              | 3            | 12           | 1.02285        | 0.4169         |
| Bare Soil          | 1            | 31           | 0.77185        | 0.3864         |

Table D. Anova output of the fitted linear mixed-effects model without bare soil. *lme(Albedo ~ Type of Vegetation + Day of Year + Month, random=~1|Site, method="ML")*

| <b>Model 4</b>     | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|--------------------|--------------|--------------|----------------|----------------|
| (Intercept)        | 1            | 32           | 49.94585       | <.0001         |
| Type of Vegetation | 2            | 32           | 7.85764        | 0.0017         |
| Day of Year        | 1            | 12           | 2.18363        | 0.1652         |
| Month              | 3            | 12           | 0.91066        | 0.4648         |

Table E. Anova output of the fitted linear mixed-effects model without month. *lme(Albedo ~ Type of Vegetation + Day of Year, random=~1|Site, method="ML")*

| <b>Model 5</b>     | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|--------------------|--------------|--------------|----------------|----------------|
| (Intercept)        | 1            | 32           | 447.4836       | <.0001         |
| Type of Vegetation | 2            | 32           | 7.9027         | 0.0016         |
| Day of Year        | 1            | 15           | 0.2563         | 0.6200         |

Table F. Anova output of the fitted linear mixed-effects model without month. *lme(Albedo ~ Type of Vegetation + Day of Year, random=~1|Site, method="ML")*

| <b>Model 6</b>     | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|--------------------|--------------|--------------|----------------|----------------|
| (Intercept)        | 1            | 32           | 1442.0135      | <.0001         |
| Type of Vegetation | 2            | 32           | 8.0271         | 0.0015         |



Table G. Anova output of the generalized least squares model without site as random factor.  
*gls(Albedo ~ Type of Vegetation, method="ML")*

| Model 7            | numDF | F-value   | p-value |
|--------------------|-------|-----------|---------|
| (Intercept)        | 1     | 1442.0135 | <.0001  |
| Type of Vegetation | 2     | 8.0271    | 0.001   |

Table H. Comparison between all the models using AIC

|         | DF | AIC       |
|---------|----|-----------|
| Model 1 | 12 | -243.3616 |
| Model 2 | 11 | -245.3291 |
| Model 3 | 10 | -246.6984 |
| Model 4 | 9  | -247.7910 |
| Model 5 | 6  | -250.7188 |
| Model 6 | 5  | -252.4414 |
| Model 7 | 4  | -254.4414 |

Table I. Summary of the final model

*Linear mixed-effects model fit by REML*

| AIC        | BIC       | logLik  |
|------------|-----------|---------|
| - 225.5941 | -216.2381 | 117.797 |

*Random effects:*

| Formula: ~1   Site | (Intercept)  | Residual |
|--------------------|--------------|----------|
| StdDev             | 6.257336e-07 | 0.019033 |

*Fixed Effects: Albedo ~ Type of Vegetation*

|                          | Value       | Std.Error   | DF | t-value  | p-value |
|--------------------------|-------------|-------------|----|----------|---------|
| (Intercept)              | 0.17529412  | 0.004616179 | 32 | 37.97385 | 0.0000  |
| Type of Vegetation Tall  | 0.00058824  | 0.006528263 | 32 | 0.09011  | 0.9288  |
| Type of Vegetation Woody | -0.02235294 | 0.006528263 | 32 | -3.42403 | 0.0017  |

*Correlation:*

|                          | (Intr) | PltTII |
|--------------------------|--------|--------|
| Type of Vegetation Tall  | -0.707 |        |
| Type of Vegetation Woody | -0.707 | 0.500  |

Standardized Within-Group Residuals:

| Min        | Q1         | Med       | Q3        | Max       |
|------------|------------|-----------|-----------|-----------|
| -2.7815473 | -0.8035581 | 0.2163426 | 0.7417460 | 2.8433595 |

|                        |    |
|------------------------|----|
| Number of Observations | 51 |
| Number of Groups       | 17 |

### III. Extra Sites (plus 3 Fixed Sites) tested interactions

Table A. Anova output of the model testing the interaction between vegetation type and woody plants cover. *lme(Albedo ~ Type of Vegetation + Woody Plants Cover + Plot : Woody Plants Cover, random=~1|Site)*

| Model Interaction 1                     | numDF | denDF | F-value   | p-value |
|---|-------|-------|-----------|---------|
| (Intercept)                             | 1     | 29    | 1128.6347 | <.0001  |
| Type of Vegetation                      | 2     | 29    | 0.6572    | 0.5258  |
| Woody Plants Cover                      | 1     | 29    | 0.0234    | 0.8795  |
| Type of Vegetation : Woody Plants Cover | 2     | 29    | 0.4222    | 0.6596  |

Table B. Anova output of the model testing the interaction between vegetation type and vegetation height. *lme(Albedo ~ Type of Vegetation + Vegetation Height + Type of Vegetation : Vegetation Height, random=~1|Site)*

| Model Interaction 2                    | numDF | denDF | F-value   | p-value |
|--|-------|-------|-----------|---------|
| (Intercept)                            | 1     | 29    | 249.42178 | <.0001  |
| Type of Vegetation                     | 2     | 29    | 1.77726   | 0.1870  |
| Vegetation Height                      | 1     | 29    | 0.35288   | 0.5571  |
| Type of Vegetation : Vegetation Height | 2     | 29    | 0.20868   | 0.8129  |

Table C. Anova output of the model testing the interaction between vegetation type and percentage of bare soil. *lme(Albedo ~ Type of Vegetation + Bare Soil + Type of Vegetation : Bare Soil, random=~1|Site)*

| Model Interaction 3            | numDF | denDF | F-value  | p-value |
|--------------------------------|-------|-------|----------|---------|
| (Intercept)                    | 1     | 29    | 650.5543 | <.0001  |
| Type of Vegetation             | 2     | 29    | 4.8273   | 0.0155  |
| Bare Soil                      | 1     | 29    | 1.3055   | 0.2626  |
| Type of Vegetation : Bare Soil | 2     | 29    | 1.9454   | 0.1611  |

Table D. Anova output of the model testing the interaction between vegetation type and month. *lme(Albedo ~ Type of Vegetation + Month + Type of Vegetation : Month, random=~1/Site)*

| <b>Model Interaction 4</b> | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|----------------------------|--------------|--------------|----------------|----------------|
| (Intercept)                | 1            | 26           | 784.8196       | <.0001         |
| Type of Vegetation         | 2            | 26           | 6.3244         | 0.0058         |
| Month                      | 3            | 13           | 0.5686         | 0.6454         |
| Type of Vegetation : Month | 6            | 26           | 0.5400         | 0.7729         |

Table E. Anova output of the model testing the interaction between vegetation type and day of year. *lme(Albedo ~ Type of Vegetation + Day of Year + Type of Vegetation : Day of Year, random=~1/Site)*

| <b>Model Interaction 5</b>       | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|----------------------------------|--------------|--------------|----------------|----------------|
| (Intercept)                      | 1            | 30           | 221.39010      | <.0001         |
| Type of Vegetation               | 2            | 30           | 2.43396        | 0.1048         |
| Day of Year                      | 1            | 15           | 2.27967        | 0.1519         |
| Type of Vegetation : Day of Year | 2            | 30           | 1.24949        | 0.3011         |

#### IV. Fixed Sites Model Simplification

Table A. Anova output of the fitted linear mixed-effects model with vegetation type, day of year, month, woody plants cover, bare soil and vegetation height as fixed effects and site as random effect. *lme(Albedo ~ Type of Vegetation + Month + Woody Plants Cover + Bare Soil + Vegetation Height + Type of Vegetation:Month, random=~1/Site/Type of Vegetation , method="ML")*

| <b>Model 1</b>          | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|-------------------------|--------------|--------------|----------------|----------------|
| (Intercept)             | 1            | 66           | 288.92681      | <.0001         |
| Type of Vegetation      | 2            | 10           | 0.09028        | 0.9144         |
| Month                   | 1            | 66           | 3.71530        | 0.0582         |
| Woody Plants Cover      | 1            | 66           | 1.61376        | 0.2084         |
| Bare Soil               | 1            | 66           | 11.85642       | 0.0010         |
| Vegetation Height       | 1            | 66           | 4.54168        | 0.0368         |
| Vegetation Type : Month | 2            | 66           | 2.67909        | 0.0761         |

Table B. Anova output of the fitted linear mixed-effects model without woody plants cover. *lme(Albedo ~ Type of Vegetation + Month + Bare Soil + Vegetation Height + Type of Vegetation:Month, random=~1|Site/Type of Vegetation , method="ML")*

| Model 2                 | numDF | denDF | F-value   | p-value |
|-------------------------|-------|-------|-----------|---------|
| (Intercept)             | 1     | 67    | 281.34511 | <.0001  |
| Type of Vegetation      | 2     | 10    | 0.68708   | 0.5253  |
| Month                   | 1     | 67    | 3.67554   | 0.0595  |
| Bare Soil               | 1     | 67    | 12.55390  | 0.0007  |
| Vegetation Height       | 1     | 67    | 6.51469   | 0.0130  |
| Vegetation Type : Month | 2     | 67    | 1.92058   | 0.1545  |

Table C. Anova output of the fitted linear mixed-effects model without type of vegetation and type of vegetation : month interaction.

*lme(Albedo ~ Month + Bare Soil + Vegetation Height, random=~1|Site/Type of Vegetation , method="ML")*

| Model 3           | numDF | denDF | F-value  | p-value |
|-------------------|-------|-------|----------|---------|
| (Intercept)       | 1     | 69    | 359.4903 | <.0001  |
| Month             | 1     | 69    | 1.6787   | 0.1994  |
| Bare Soil         | 1     | 69    | 24.0025  | <.0001  |
| Vegetation Height | 1     | 69    | 0.0147   | 0.9039  |

Table D. Anova output of the fitted linear mixed-effects model without vegetation height.

*lme(Albedo ~ Month + Bare Soil, random=~1|Site/Type of Vegetation , method="ML")*

| Model 4     | numDF | denDF | F-value  | p-value |
|-------------|-------|-------|----------|---------|
| (Intercept) | 1     | 70    | 428.0453 | <.0001  |
| Month       | 1     | 70    | 1.7307   | 0.1926  |
| Bare Soil   | 1     | 70    | 28.2999  | <.0001  |

Table E. Anova output of the fitted linear mixed-effects model without month. *lme(Albedo ~ Bare Soil, random=~1|Site/Type of Vegetation , method="ML")*

| Model 5     | numDF | denDF | F-value   | p-value |
|-------------|-------|-------|-----------|---------|
| (Intercept) | 1     | 71    | 2242.6951 | <.0001  |
| Bare Soil   | 1     | 71    | 88.7082   | <.0001  |

Table F. Comparison between all the models using AIC

|         | DF | AIC       |
|---------|----|-----------|
| Model 1 | 12 | -466.9818 |
| Model 2 | 11 | -467.7986 |
| Model 3 | 7  | -461.6277 |
| Model 4 | 6  | -463.6187 |
| Model 5 | 5  | -463.8801 |

Table H. Summary of the final model

*Linear mixed-effects model fit by REML*

| AIC       | BIC       | logLik   |
|-----------|-----------|----------|
| -378.1373 | -351.6634 | 200.0687 |

*Random effects:*

| Formula: ~1   Site (Intercept)                                  |                       |
|---|-----------------------|
| StdDev  | 0.00665177            |
| Formula: ~1   Type of Vegetation %in% Site (Intercept) Residual |                       |
| StdDev  | 0.008519698 0.0147539 |

*Fixed effects: Albedo ~ Type of Vegetation + Month + Bare Soil + Vegetation Height + Type of Vegetation : Month*

|                                  | Value       | Std. Error  | DF | t-value   | p-value |
|----------------------------------|-------------|-------------|----|-----------|---------|
| (Intercept)                      | 0.15467857  | 0.009327546 | 67 | 16.582987 | 0.0000  |
| Type of Vegetation Tall          | -0.00261908 | 0.010371466 | 10 | -0.252528 | 0.8057  |
| Type of Vegetation Woody         | -0.01323305 | 0.011630469 | 10 | -1.137792 | 0.2817  |
| Month                            | 0.00406708  | 0.002084500 | 67 | 1.951106  | 0.0552  |
| Bare Soil                        | -0.00077683 | 0.000220738 | 67 | -3.519251 | 0.0008  |
| Vegetation Height                | 0.00044090  | 0.000167559 | 67 | 2.631340  | 0.0105  |
| Type of Vegetation Tall : Month  | -0.00209088 | 0.002888166 | 67 | -0.723947 | 0.4716  |
| Type of Vegetation Woody : Month | -0.00576299 | 0.002962016 | 67 | -1.945631 | 0.0559  |

*Correlation:*

|                                  | <b>(Intr)</b> | <b>Ty..VT</b> | <b>Ty..VW</b> | <b>Month</b> | <b>Bare Soil</b> | <b>Veg. Height</b> | <b>T..VT</b> |
|----------------------------------|---------------|---------------|---------------|--------------|------------------|--------------------|--------------|
| Type of Vegetation Tall          | -0.439        |               |               |              |                  |                    |              |
| Type of Vegetation Woody         | -0.226        | 0.501         |               |              |                  |                    |              |
| Month                            | -0.781        | 0.430         | 0.290         |              |                  |                    |              |
| Bare Soil                        | -0.561        | -0.179        | -0.432        | 0.401        |                  |                    |              |
| Vegetation Height                | -0.310        | -0.054        | -0.389        | 0.130        | 0.468            |                    |              |
| Type of Vegetation Tall : Month  | 0.389         | -0.750        | -0.275        | -0.555       | 0.061            | -0.286             |              |
| Type of Vegetation Woody : Month | 0.334         | -0.393        | -0.612        | -0.504       | 0.144            | -0.277             | 0.572        |

*Standardized Within-Group Residuals:*

| <b>Min</b>  | <b>Q1</b>   | <b>Med</b> | <b>Q3</b>  | <b>Max</b> |
|-------------|-------------|------------|------------|------------|
| -2.18807762 | -0.68235798 | 0.04779991 | 0.69839814 | 1.71335649 |

|                        |      |                              |
|------------------------|------|------------------------------|
| Number of Observations | 90   |                              |
|                        | Site | Type.of.Vegetation %in% Site |
| Number of Groups       | 6    | 18                           |

## V. Woody Plants Recruitment Model Simplification

Table A. Anova output of the fitted linear mixed-effects model with grassland type, height class, area, DPM, % of lawn, % of forbs, % of bunch grass, % of bare soil as fixed effects, an interaction between grassland type and height class, and site as random effect.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Area + DPM + Lawn + Bunch + Forbs + Bare.Soil + Height.Class:Grassland.Type, random=~1|Site, method="ML")*

| Model 1                       | numDF | denDF | F-value   | p-value |
|-------------------------------|-------|-------|-----------|---------|
| (Intercept)                   | 1     | 261   | 1.905040  | 0.1687  |
| Grassland Type                | 1     | 261   | 4.670234  | 0.0316  |
| Height Class                  | 3     | 261   | 12.621193 | <.0001  |
| Area                          | 1     | 37    | 2.480943  | 0.1237  |
| DPM                           | 1     | 261   | 0.021967  | 0.8823  |
| % Lawn                        | 1     | 261   | 0.928485  | 0.3361  |
| % Bunch                       | 1     | 261   | 0.120738  | 0.7285  |
| % Forbs                       | 1     | 261   | 0.008476  | 0.9267  |
| % Bare Soil                   | 1     | 261   | 1.817158  | 0.1788  |
| Grassland Type : Height Class | 3     | 261   | 2.791012  | 0.0410  |

Table B. Anova output of the fitted linear mixed-effects model without % of forbs.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Area + DPM + Lawn + Bunch + Bare.Soil + Height.Class:Grassland.Type, random=~1|Site, method="ML")*

| Model 2                       | numDF | denDF | F-value   | p-value |
|-------------------------------|-------|-------|-----------|---------|
| (Intercept)                   | 1     | 262   | 2.341289  | 0.1272  |
| Grassland Type                | 1     | 262   | 6.467466  | 0.0116  |
| Height Class                  | 3     | 262   | 12.664129 | <.0001  |
| Area                          | 1     | 37    | 2.480063  | 0.1238  |
| DPM                           | 1     | 262   | 0.020849  | 0.8853  |
| % Lawn                        | 1     | 262   | 1.839686  | 0.1762  |
| % Bunch                       | 1     | 262   | 0.119868  | 0.7295  |
| % Bare Soil                   | 1     | 262   | 1.940197  | 0.1648  |
| Grassland Type : Height Class | 3     | 262   | 2.800506  | 0.0405  |

Table C. Anova output of the fitted linear mixed-effects model without DPM.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Area + Lawn + Bunch + Bare.Soil + Height.Class:Grassland.Type, random=~1|Site, method="ML")*

| <b>Model 3</b>                | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|-------------------------------|--------------|--------------|----------------|----------------|
| (Intercept)                   | 1            | 263          | 2.622853       | 0.1065         |
| Grassland Type                | 1            | 263          | 7.027291       | 0.0085         |
| Height Class                  | 3            | 263          | 12.700159      | <.0001         |
| Area                          | 1            | 37           | 2.508640       | 0.1217         |
| % Lawn                        | 1            | 263          | 1.828406       | 0.1775         |
| % Bunch                       | 1            | 263          | 0.121401       | 0.7278         |
| % Bare Soil                   | 1            | 263          | 1.930110       | 0.1659         |
| Grassland Type : Height Class | 3            | 263          | 2.808474       | 0.0400         |

Table D. Anova output of the fitted linear mixed-effects model without % of bunch grass.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Area + Lawn + Bare.Soil + Height.Class:Grassland.Type, random=~1|Site, method="ML")*

| <b>Model 4</b>                | <b>numDF</b> | <b>denDF</b> | <b>F-value</b> | <b>p-value</b> |
|-------------------------------|--------------|--------------|----------------|----------------|
| (Intercept)                   | 1            | 264          | 34.63815       | <.0001         |
| Grassland Type                | 1            | 264          | 6.93209        | 0.0090         |
| Height Class                  | 3            | 264          | 12.73324       | <.0001         |
| Area                          | 1            | 37           | 2.65993        | 0.1114         |
| % Lawn                        | 1            | 264          | 3.59689        | 0.0590         |
| % Bare Soil                   | 1            | 264          | 2.80650        | 0.0951         |
| Grassland Type : Height Class | 3            | 264          | 2.81579        | 0.0396         |



Table E. Anova output of the fitted linear mixed-effects model without area.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Lawn + Bare.Soil + Height.Class:Grassland.Type, random=~1/Site, method="ML")*

| Model 5                       | numDF | denDF | F-value  | p-value |
|-------------------------------|-------|-------|----------|---------|
| (Intercept)                   | 1     | 264   | 36.57361 | <.0001  |
| Grassland Type                | 1     | 264   | 7.41604  | 0.0069  |
| Height Class                  | 3     | 264   | 12.78212 | <.0001  |
| % Lawn                        | 1     | 264   | 3.94240  | 0.0481  |
| % Bare Soil                   | 1     | 264   | 3.33439  | 0.0690  |
| Grassland Type : Height Class | 3     | 264   | 2.82660  | 0.0391  |

Table F. Anova output of the fitted linear mixed-effects model without bare soil.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Lawn + Height.Class:Grassland.Type, random=~1/Site, method="ML")*

| Model 6                       | numDF | denDF | F-value  | p-value |
|-------------------------------|-------|-------|----------|---------|
| (Intercept)                   | 1     | 265   | 44.00082 | <.0001  |
| Grassland Type                | 1     | 265   | 4.14498  | 0.0428  |
| Height Class                  | 3     | 265   | 12.65754 | <.0001  |
| % Lawn                        | 1     | 265   | 1.40706  | 0.2366  |
| Grassland Type : Height Class | 3     | 265   | 2.79905  | 0.0405  |

Table G. Anova output of the fitted linear mixed-effects model without % of lawn.

*lme(Woody.Plants ~ Grassland.Type + Height.Class + Height.Class:Grassland.Type, random=~1/Site, method="ML")*

| Model 7                       | numDF | denDF | F-value  | p-value |
|-------------------------------|-------|-------|----------|---------|
| (Intercept)                   | 1     | 266   | 50.34482 | <.0001  |
| Grassland Type                | 1     | 266   | 19.05821 | <.0001  |
| Height Class                  | 3     | 266   | 12.66983 | <.0001  |
| Grassland Type : Height Class | 3     | 266   | 2.80177  | 0.0404  |

Table H. Comparison between all the models using AIC

|         | DF | AIC       |
|---------|----|-----------|
| Model 1 | 16 | -101.0961 |
| Model 2 | 15 | -103.0872 |
| Model 3 | 14 | -105.0657 |
| Model 4 | 13 | -106.9396 |
| Model 5 | 12 | -106.2843 |
| Model 6 | 11 | -104.8633 |
| Model 7 | 10 | -105.4235 |

Table I. Anova output of the chosen final model. *lme*(Woody.Plants ~ Grassland.Type + Height.Class + Height.Class:Grassland.Type, random=~1|Site, method="REML")

| Model 7                       | numDFdenDF |     | F-value  | p-value |
|-------------------------------|------------|-----|----------|---------|
| (Intercept)                   | 1          | 266 | 50.34482 | <.0001  |
| Grassland Type                | 1          | 266 | 19.05821 | <.0001  |
| Height Class                  | 3          | 266 | 12.66983 | <.0001  |
| Grassland Type : Height Class | 3          | 266 | 2.80177  | 0.0404  |

Table J. Summary of the final model

Linear mixed-effects model fit by REML

| AIC       | BIC       | logLik   |
|-----------|-----------|----------|
| -62.22993 | -25.05965 | 41.11496 |

Random effects:

| Formula: ~1   Site | (Intercept) | Residual  |
|--------------------|-------------|-----------|
| StdDev             | 0.07098667  | 0.1914115 |

*Fixed effects: Woody.Plants ~ Grassland.Type + Height.Class + Height.Class:Grassland.Type*

|                                   | Value       | Std. Error | DF  | t-value   | p-value |
|-----------------------------------|-------------|------------|-----|-----------|---------|
| (Intercept)                       | 0.13538462  | 0.01908060 | 266 | 7.095408  | 0.0000  |
| Grassland.TypeLawn                | -0.09461538 | 0.02167308 | 266 | -4.365571 | 0.0000  |
| Height.Class.L                    | -0.11123005 | 0.03065037 | 266 | -3.628996 | 0.0003  |
| Height.Class.Q                    | -0.11948718 | 0.03065037 | 266 | -3.898393 | 0.0001  |
| Height.Class.C                    | 0.09517623  | 0.03065037 | 266 | 3.105223  | 0.0021  |
| Grassland.TypeLawn:Height.Class.L | 0.05962848  | 0.04334617 | 266 | 1.375634  | 0.1701  |
| Grassland.TypeLawn:Height.Class.Q | 0.09205128  | 0.04334617 | 266 | 2.123632  | 0.0346  |
| Grassland.TypeLawn:Height.Class.C | -0.06134853 | 0.04334617 | 266 | -1.415316 | 0.1581  |

*Correlation:*

|                                   | (Intr)  | Grs.TL | Hg.C.L  | Hg.C.Q  | Hg.C.C  |
|-----------------------------------|---------|--------|---------|---------|---------|
| Grassland.TypeLawn                | - 0.568 |        |         |         |         |
| Height.Class.L                    | 0.000   | 0.000  |         |         |         |
| Height.Class.Q                    | 0.000   | 0.000  | 0.000   |         |         |
| Height.Class.C                    | 0.000   | 0.000  | 0.000   | 0.000   |         |
| Grassland.TypeLawn:Height.Class.L | 0.000   | 0.000  | - 0.707 | 0.000   | 0.000   |
| Grassland.TypeLawn:Height.Class.Q | 0.000   | 0.000  | 0.000   | - 0.707 | 0.000   |
| Grassland.TypeLawn:Height.Class.C | 0.000   | 0.000  | 0.000   | 0.000   | - 0.707 |

**G. TL : H.C.L   G. TL : H.C.Q**

(Intercept)

Grassland.TypeLawn

Height.Class.L

Height.Class.Q

Height.Class.C

Grassland.TypeLawn:Height.Class.L

Grassland.TypeLawn:Height.Class.Q   0.000

Grassland.TypeLawn:Height.Class.C   0.000   0.000

Standardized Within-Group Residuals:

| Min         | Q1          | Med         | Q3         | Max        |
|-------------|-------------|-------------|------------|------------|
| -1.63536350 | -0.37275842 | -0.08451691 | 0.13523188 | 8.52532161 |

|                        |     |
|------------------------|-----|
| Number of Observations | 312 |
| Number of Groups       | 39  |

Table K. Anova output of the chosen final model, using lawn grassland as intercept.  
*lme(Woody.Plants ~ Grassland.Type + Height.Class + Height.Class:Grassland.Type, random=~1|Site, method="REML")*

| Model 7                       | numDFdenDF |     | F-value   | p-value |
|-------------------------------|------------|-----|-----------|---------|
| (Intercept)                   | 1          | 266 | 4.565425  | 0.0335  |
| Grassland Type                | 1          | 266 | 19.058211 | <.0001  |
| Height Class                  | 3          | 266 | 1.617893  | 0.1855  |
| Grassland Type : Height Class | 3          | 266 | 2.801767  | 0.0404  |

Table L. Summary of the final model with lawn as intercept

Linear mixed-effects model fit by REML

|           |           |          |
|-----------|-----------|----------|
| AIC       | BIC       | logLik   |
| -62.22993 | -25.05965 | 41.11496 |

Random effects:

| Formula: ~1   Site | (Intercept) | Residual  |
|--------------------|-------------|-----------|
| StdDev             | 0.07098666  | 0.1914115 |

*Fixed effects: Woody.Plants ~ Grassland.Type + Height.Class + Height.Class:Grassland.Type*

|                                   | Value       | Std. Error | DF  | t-value   | p-value |
|-----------------------------------|-------------|------------|-----|-----------|---------|
| (Intercept)                       | 0.04076923  | 0.01908059 | 266 | 2.136686  | 0.0335  |
| Grassland.TypeBunch               | 0.09461538  | 0.02167308 | 266 | 4.365571  | 0.0000  |
| Height.Class.L                    | -0.05160157 | 0.03065037 | 266 | -1.683555 | 0.0934  |
| Height.Class.Q                    | -0.02743590 | 0.03065037 | 266 | -0.895125 | 0.3715  |
| Height.Class.C                    | 0.03382770  | 0.03065037 | 266 | 1.103664  | 0.2707  |
| Grassland.TypeLawn:Height.Class.L | -0.05962848 | 0.04334617 | 266 | -1.375634 | 0.1701  |
| Grassland.TypeLawn:Height.Class.Q | -0.09205128 | 0.04334617 | 266 | -2.123631 | 0.0346  |
| Grassland.TypeLawn:Height.Class.C | 0.06134853  | 0.04334617 | 266 | 1.415316  | 0.1581  |

*Correlation:*

|                                   | (Intr) | Grs.TL | Hg.C.L | Hg.C.Q | Hg.C.C |
|-----------------------------------|--------|--------|--------|--------|--------|
| Grassland.TypeLawn                | -0.568 |        |        |        |        |
| Height.Class.L                    | 0.000  | 0.000  |        |        |        |
| Height.Class.Q                    | 0.000  | 0.000  | 0.000  |        |        |
| Height.Class.C                    | 0.000  | 0.000  | 0.000  | 0.000  |        |
| Grassland.TypeLawn:Height.Class.L | 0.000  | 0.000  | -0.707 | 0.000  | 0.000  |
| Grassland.TypeLawn:Height.Class.Q | 0.000  | 0.000  | 0.000  | -0.707 | 0.000  |
| Grassland.TypeLawn:Height.Class.C | 0.000  | 0.000  | 0.000  | 0.000  | -0.707 |

|                                   | G. TL : H.C.L | G. TL : H.C.Q |
|-----------------------------------|---------------|---------------|
| (Intercept)                       |               |               |
| Grassland.TypeLawn                |               |               |
| Height.Class.L                    |               |               |
| Height.Class.Q                    |               |               |
| Height.Class.C                    |               |               |
| Grassland.TypeLawn:Height.Class.L |               |               |
| Grassland.TypeLawn:Height.Class.Q | 0.000         |               |
| Grassland.TypeLawn:Height.Class.C | 0.000         | 0.000         |

*Standardized Within-Group Residuals:*

| <b>Min</b>  | <b>Q1</b>   | <b>Med</b>  | <b>Q3</b>  | <b>Max</b> |
|-------------|-------------|-------------|------------|------------|
| -1.63536332 | -0.37275839 | -0.08451689 | 0.13523185 | 8.52532169 |

|                        |     |
|------------------------|-----|
| Number of Observations | 312 |
| Number of Groups       | 39  |

## SENASTE UTGIVNA NUMMER

- 2017:9      Prevalence of *Borrelia burgdorferi* sensu latu in rodents from two areas with varying wild ungulate densities in Southern Sweden  
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Författare: Therese Arvén Norling
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Författare: Julia L. Jansson
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Författare: Rebecka Strömbom
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- 2017:15     Analysing the seal-fishery conflict in the Baltic Sea and exploring new ways of looking at marine mammal movement data  
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Författare: Sabrina Mittl
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